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CONTENTS OF VOLUME V.

No. 1.—The Dakota-Permian Contact in Northern Kansas... *F. C. Greene.*

2.—Further Notes on the Pueblo Ruins of Scott County, *H. T. Martin.*

3.—The Influence of Magnesium Sulphate on the Motor Cells of the Cerebral Cortex.... *H. F. Hyndman and W. E. Mitchner.*

4.—A Study of the Respiratory and Cardiac Activities of the Skate following Intravenous Injection of Salt Solution... *Ida Hyde.*

5.—Nutrition of the Embryo Sac and Embryo in Certain Labiatæ, *F. H. Billings.*

6.—Mitosis in the Root Tips of Podophyllum peltatum, *Aute Richards.*

7.—Koeberlinia spinosa Zucc. : An Ecological Study of the Anatomy of the Stem and some other parts.. *Miriam Sheldon.*

8.—A Case of Absolute Tone Memory..... *Archibald Hogg.*

9.—The Hackberry Psylla, Pachypsylla celtidis-mammæ Riley: A Study in Comparative Insect Morphology ..... *H. B. Stowe.*

10.—Investigations Regarding the Phloëm and Food Conduction in Plants..... *Frank U. G. Agrelius.*

11.—Histology of Townsendia exscapa and Lesquerella spathulata, *Lillian Bunton.*

12.—Cell Changes in the Alveoli of a Carcinoma of the Mamma, *Earl F. Clark.*

13.—The Temnospondylous Amphibia and a New Species of Eryops from the Permian of Oklahoma..... *Roy L. Moodie.*

14.—An Armored Dinosaur from the Cretaceous of Wyoming..... *Roy L. Moodie.*

15.—A Contribution to the Soft Anatomy of Cretaceous Fishes, and a New Promitive Herring-like fish from the Texas Cretaceous ..... *Roy L. Moodie.*

16.—A New Species of Holotrich..... *Nadine Nowlin.*

17.—Orthoptera from the Santa Rita Mountains, Arizona, collected by the University of Kansas Expedition..... *Jas. A. G. Rehn.*

18.—Observations on the Gryllidæ: III. Notes of the Classification and Some Habits of Certain Crickets, *W. J. Baumgartner.*

19.—Observations on the Gryllidæ: IV. Copulation, *W. J. Baumgartner.*

20.—An Examination of the Chromosomes of Anasa tristis..... *C. E. McClung and Edith Pinney.*

21.—Foundations of Arithmetic ..... *Arthur Bolles Frisell.*

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NOTICE TO EXCHANGES.

The attention of learned societies and other institutions which exchange scientific publications with the University of Kansas is called to the list of publications of this University on the third page of the cover of this issue.

Those marked "Supply exhausted" cannot be furnished at all; those marked "Supply small" cannot be furnished separately; those marked "Supply large" will gladly be furnished to any of our exchanges who may need them to complete their files.

Back numbers of the *Kansas University Quarterly* and *Geological Survey*, as far as possible, will be sent to those of our newer correspondents who are able and willing to reciprocate.

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The *Kansas University Science Bulletin* (continuation of the *Kansas University Quarterly*) is issued in parts at irregular intervals. One volume, containing from 300 to 400 pages of reading-matter, with necessary illustrations, is issued each year. The subscription price is $3 per volume. Exchanges with other institutions and learned societies everywhere are solicited. All *exchanges* should be addressed to the LIBRARY OF THE UNIVERSITY OF KANSAS.

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CONTENTS:

THE DAKOTA-PERMIAN CONTACT IN NORTHERN KANSAS, . *F. C. Greene.*

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THE DAKOTA-PERMIAN CONTACT IN NORTHERN KANSAS.

BY F. C. GREENE.

Plates I to IV.

INTRODUCTION.

DURING the summer of 1906, while working on the University Geological Survey of Kansas, under the direction of Dr. J. W. Beede, the Permian-Cretaceous contact in Kansas, north of the Smoky Hill river, was mapped. The most of the northern third of the region was mapped jointly with Doctor Beede and the remainder mapped individually, in alternate stretches.

The region covered in this account lies in Washington, Riley, Clay, Dickinson and Ottawa counties, and is included in the Washington, Marysville, Clay Center, Abilene, and a corner of the Minneapolis topographic sheets of the U. S. Geological Survey. The area lies in the drainage basins of the Little Blue, Republican, Smoky Hill and Solomon rivers.

The topography is characterized by bold bluffs of the Dakota sandstone and smaller benches of the harder Permian limestones and shales. There is one peculiar feature of the topography throughout the region: northern slopes of the divides are generally steep, while the southern slopes are very gradual, and often without rock exposures. The effect is as if the land had been tipped to the south, or as if there had been an interruption of a southeastern drainage which turned the master streams to the east, thereby causing the streams to erode their southern banks.

In regions of the Dakota formation, this often results in

an extensive series of low hills, composed entirely of loose sand, such as are seen in the vicinity of Abilene.

In the extreme northern part of the state, the country-rock is overlain by the glacial drift of the Kansan ice sheet. At the points where the contact crosses the Kansas-Nebraska line, the original topography and geology are obscured by drift, 60 to 100 feet in thickness, as observed from well borings.

GENERAL SECTION.

Pleistocene.—Glacial drift of Kansas sheet and loess (?) terraces.

Cretaceous.—Dakota formation, sandstones and clays.

Permian.—Limestones and shales.

Permian.—No attempt was made to distinguish between the formations of the Permian, but it was necessary to note such local aspects as would help in determining the contact line. There is everywhere an unconformity of considerable relief between the Permian and Cretaceous systems; which represents in time the Upper Permian, Triassic, Jurassic and Comanche Cretaceous.

The relief of this unconformity amounts, in places, to nearly 100 feet in the distance of a quarter of a mile. In one place (two miles northeast of Emmons, Washington county) there is a Permian monadnock which has patches of Dakota lying here and there on its sides, owing to erosion since Dakota times. This results in exposures of Permian above the level of the surrounding Dakota. Similar conditions on a smaller scale are found elsewhere.

Owing to this unconformity, the section of the Permian differs in places, the Permian having been eroded before the deposition of the Dakota to a lower horizon in some places than in others. The result of this is that the Permian is represented at the contact by different horizons, none of which are present over very large areas. At most places a series of thin-bedded limestones and shales was present at the contact, but in others a very porous limestone, evenly bedded red and yellow shales, or blue clay shales, represent the horizon of the Permian present at the contact. Over the whole area the Permian beds appear to be very evenly stratified.

The following section, taken from a cut on the Burlington railroad about two miles northwest of Hanover, Washington

county, shows a typical succession of the Permian beds of that region:

10.	Limestone, thin-bedded, and yellowish shales	5 ft.
9.	Limestone, massive	6 in.
8.	Shales, calcareous olive-gray, with limestone about four feet from bottom	16 ft.
7.	Limestone, grading through marly concretions to marly shales	1 ft.
6.	Shales, marly gray	4 ft.
5.	Shales, red, evenly bedded, with occasional indurated bands; in the lower portion are two layers of very impure semi-crystalline limestone or dolomite, apparently thrown down by precipitation. There are also four or five very thin layers of greenish shales	15 ft.
4.	Covered	10 ft.
3.	Limestone, two layers, separated by bluish shale; upper limestone hard	3½ ft.
2.	Shales, olive, indurated	4 ft.
1.	Shales, yellow calcareous and argillaceous limestone	2 ft.
	Covered slope below.	

The character of the Permian from a little different horizon is shown in a section from the north bank of Mill creek, near the middle of section 13, Charleston township, Washington county:

7.	Covered.	
6.	Limestone, light buff, cellular, rather thin-bedded	8 ft.
5.	Shales, bluish and yellowish	13 ft.
4.	Limestone, blue, laminated, fossiliferous	4 in.
3.	Shales, bluish	3 ft.
2.	Limestone, hard, buff, fossiliferous	8 in.
1.	Shale, blue, and covered slope to water level	17 ft.

Cretaceous-Dakota.—The prominent bluffs of this formation are composed of a deep-red or brown, rather coarse-grained, ferruginous sandstone. For this reason the formation is often spoken of as the Dakota sandstone, but this is a misnomer, as the bulk of the formation is probably not a hard sandstone, but clays and shales.[1] Other exposures vary greatly. In fact, it is hard to imagine a formation of a more diversified character. It gives much evidence of being a shallow-water deposit, such as would be formed along shores and in small estuaries by delta deposits, etc. Both the nature of the deposits and the fossil content bear out this statement. The land mass was probably a short distance east of the present eastern outcrop, as the Dakota becomes more evenly strat-

1. Gould. Trans. Kan. Acad. Sci., XVII, pp. 122-178. 1901.

ified to the west. The fossils consist of the leaves of such genera as Quercus, Sassafras, Salix, Ficus, Protophyllum, Platanus, Betulites, etc., all land plants.

Near the contact line the diversified nature is well shown. Yellow, red, brown and white sandstones are found, both consolidated and loose. These colors may be in separate layers or all in the same stone, in a space six inches square. In places a conglomerate predominates. In Charleston township, Washington county, about a quarter of a mile west of the line between sections 23 and 24, there are twenty-five to thirty feet of variegated, multi-colored clays, such as are typical of the Dakota a little west of Brookville, Saline county. The local name for this is "rainbow" clay, all the colors of the rainbow being jumbled into a variegated mass. There is no consistency in the structure in the easternmost outcrop of the Dakota. Within a quarter of a mile a road may cut through both a deposit of hard dark-red sandstone and a light-colored clay. In the sandstone cross-bedding is very much in evidence. In places large nodules of iron pyrites are found, while iron-oxide concretions of various sizes and shapes interest the inhabitants throughout the region.

The loose Dakota sands wash far down over the Permian and often obscure the contact.

As the sandstone is very porous, while the limestones and shales of the Permian are impervious, springs are found along the contact line and are helpful in locating it.

Pleistocene.—Glacial drift of the Kansan ice sheet. This formation overlies the five northern rows of townships in the region mapped. It is as diversified in character as the formations underlying it. Besides the sands and boulders of quartzite, greenstone, granite, etc., it is composed of fragments of Permian and Dakota rocks, the latter generally forming the bulk of the deposits. This is probably due to the fact that the Dakota formation extends some distance to the east in the region north of Kansas, thus lying directly in the path of the Kansan ice sheet. In the region of Hanover (and several other places) these materials have been cemented together into a conglomerate. Variegated clays and other clays, resembling those of the Dakota, have been deposited in places.

This causes some very perplexing problems in locating the contact in the drift-covered region. In the first place, it ob-

scures the underlying formations over large areas, and in the second, it contains deposits of clay, sand and conglomerate almost identical with those of the Dakota. However, if there are any wells present, the water will be hard in the drift and soft in the Dakota sandstone.

Other Deposits of the Pleistocene.—In much of the region along the west side of Mill creek in Washington county there are fifteen feet of very sandy, jointed clays, gray above and brown beneath, overlying the plain sloping towards the creek. This deposit may be due to the changes which seem to have been made in the direction of Mill creek in glacial times. The topography and geology suggest the possibility that Mill creek once flowed southeast from Washington, with a large branch from the north joining it just east of Washington, while a small stream used the present outlet of Mill creek into the Little Blue river. There is a channel beneath Greenleaf, nearly 100 feet deep and filled with glacial debris, as shown by the wells supplying water to Greenleaf. Along the railroad between Washington and Greenleaf there are no exposures of rock in place, but as the region was not carefully studied this evidence is not conclusive. Glacial damming of this stream in the region southeast of Washington may have formed a lake which sought an outlet to the north in the present valley of Mill creek.

If these suggestions are true, it was probably in this lake that these deposits were formed.

West of the Republican river at Clay Center the river bluffs are terraces composed of loess-like material with calcareous concretions, and native rock below. They rise to a height of forty to sixty feet at the edge of the river bottom, and are higher here than farther back. There is, as a rule, a fair back slope of the terrace to the hills of the Dakota to the west, and the junction is usually occupied by streams or branches of them and the drainage is away from the river down the terrace, which has a maximum width of three miles.

It may be that this deposit is the same material as that which is known as "plains marl" in the western part of the state. In regard to the latter, Professor Haworth[2] believes it to have had the same origin as that of the Tertiary mortar

2. Univ. Geol. Surv. of Kan., vol. II, p. 275.

beds, and thinks it probable that many of the properties of the plains marl are largely due to the action of wind.

In the region mapped the loess was found in valleys having a north-and-south direction. This may be due to the fact that a wind from the west, carrying the material, would deposit it in valleys lying north and south, while it would not accumulate in valleys having an east-and-west direction.

DISCUSSION OF THE MAPPING.

The mapping began at the Kansas-Nebraska line. Here the contact was concealed by 60 to 100 feet of drift. Just west of the Little Blue river, opposite Hollenberg, the Permian was exposed near the 1300-foot contour, while east of this town the Dakota rocks were exposed near the same level. Thus, in a general way, the contact is at the 1300-foot level between the state line and Washington west of the Little Blue. On the west bank of Mill creek there is a deposit of Pleistocene, covering the slope. The region is mapped as Cretaceous rock, though there is little doubt that it is material washed from the higher hills to the west. A tongue of Dakota extends north in the area between Mill creek and this river. If the suggestion that Mill creek formerly had its outlet to the south is true, this tongue would probably be an outlier.

On the east side of the Little Blue are outliers within six miles north and south of Hanover, but inside the boundaries of Washington county. South of Washington the contact rises nearly to the 1400-foot line, but west of that place pitches down, so that the Permian extends up Mill creek only two miles. The contact is found in the valley of Beaver creek, at an elevation of about 1375 feet. At Greenleaf, owing to the presence of the old channel noted above, neither Permian nor Dakota is exposed, but the former is only thirty feet below the level of the town a few miles east and west. Across this area the contact is dotted.

From Greenleaf to Clifton there is a continuous dip to the west. There is an outlier of Dakota in the vicinity of Chepstow, and it also extends south into the extreme northwest corner of Riley county, south of Kimeo. West from this point to Clifton the contact lies mostly in the northern row of townships of Clay county.

In the Republican valley the contact is concealed by a de-

posit of loess-like terrace material and alluvium, but a few miles east of Clifton it is found at the 1280-foot contour, and probably crosses the river about a mile southeast of Clifton. West of the Republican river the Dakota is found as a thin sheet on the terrace, as shown by well borings. Here the contact is at about the 1240-foot mark, but rises steadily to the south until the divide south of Manchester is reached, where a height of 1360 feet is reached. There is, however, a constant westward dip, so that the contact never extends very far west in the valleys of eastward flowing streams. In the region just described the contact passes near Idana, Oak Hill, Longford and Manchester.

East of the Republican river, in Clay county, the Dakota forms a large outlier about three miles northwest of Green. Here the contact is nearly up to the 1400-foot contour. From this outlier west to the Republican river the dip of the Permian is clearly and distinctly shown.

From Manchester to Abilene the Dakota lies on a narrow divide, but at its southern extension expands into a large area. In this area it is very thin, and disappears in a large expansion of sand hills, which may have originated from poorly lithified sandstone, or from stream or wind sediments.

From Abilene east to within three miles of Chapman, sand and sand hills occur on the north side of the Smoky Hill. There is much doubt as to the origin of these deposits. In this connection, the observations of Hay[3] in the vicinity of Junction City are interesting. He found sand hills near Junction City at or about the same level as those in the vicinity of Abilene. He says: "A more recent examination of the high-level sand dunes previously referred to revealed the fact that they are residual beds, resting on and abutting against undoubted outliers of the Dakota." Two areas of Dakota are shown on his map. These are only one-half of a mile west of the easternmost outcrops in Washington county, although the trend of the eastern outcrop of the Dakota is southwest throughout the state.

3. Hay. Geol. of Ft. Riley, etc., Bull. 137, U. S. G. S., p. 23.

CONCLUSIONS.

There is an unconformity of varying, but considerable, relief between the Permian and Cretaceous systems.

The eastern part of the Dakota sediments was deposited in shallow water along the shore and in estuaries and lagoons, as shown by the nature of the formation and the fossil content. Some of them may be of sub-ærial origin.

The shore-line of the Cretaceous sea was probably some distance to the east of the main body of the Dakota outcrop, as is shown by the presence of outcrops east of Hanover, Washington county, and in the vicinity of Junction City.

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FURTHER NOTES ON THE PUEBLO RUINS OF SCOTT COUNTY.

BY H. T. MARTIN.

(Contribution from the Zoölogical Laboratory, No. 188.)

Plates V to IX, and one text figure.

AT the annual meeting of the Kansas State Historical Society at Topeka in January, 1899, Dr. S. W. Williston read before that body a paper entitled "Some Pueblo Ruins in Scott County, Kansas," in which was fully set forth the results of the excavation of the ruins now known as Quartelejo, together with a list of the implements and weapons procured from the rooms which composed the old building. This paper will be found in the Kansas Historical Collections, volume 6, 1897-1900. Unfortunately it was not then possible to publish along with the paper the photographs and drawings of the ruins which were made during the excavation. In order to make the photographs and ground-plan drawing which accompany this paper as comprehensible as possible, the original description by Doctor Williston will be given almost verbatim. Since this account was based upon the field notes of the present writer, who made the excavations under the directions of Dr. Williston, its repetition here will be somewhat in the nature of a personal account.

DOCTOR WILLISTON'S ACCOUNT OF THE RUINS.

"The ruins are situated in the valley of Beaver creek (wrongly called Ladder creek on the map), in the northern part of Scott county, twelve miles due north from Scott City, and about ten miles south of the Smoky Hill river, as shown on the maps, precisely where the township line touches the

most eastern bend of the creek. At this place the valley of the creek, which here runs nearly north, is less than a mile wide, surmounted on either side by high bluffs of Tertiary material. The immediate valley is excavated in the Cretaceous chalk. The result is that here, as elsewhere in western Kansas where like geological conditions obtain, the underflow through the Tertiary sandstones, over the impervious chalk floor, comes abundantly into the valley, furnishing a considerable stream of water. Perhaps no stream in the western part of the state offers more favorable conditions for irrigation than does this in its lower part. In the dryest years there is always an abundance of water in the stream, and in the deep pools along its course there are always many fish. About a half mile above the site of the present ruins, the Tertiary underflow comes to the surface along the side of a hill in such perpetual abundance that it is utilized in the irrigation of a considerable tract of land.

"These two facts—easy facilities for unfailing and extensive irrigation, and a fish- and beaver-producing, perpetually flowing stream—are undoubtedly explanatory of the location of the ruins at this place. The ruins are situated near the middle of the valley, close to the stream, and away from any possibility of ambush by hostile savages. They occupy a small knoll of ground, and, as first seen by us, consisted of a low, rounded heap of soil and stone, perhaps 75 or 100 feet in diameter, the soil wholly overgrown by buffalo grass. The rocks are the coarse sandstone of the neighboring hills. A small excavation had been made in the middle of this mound by previous explorers, perhaps two feet in depth and of a dozen square feet in area."

In conclusion, Doctor Williston says: "One fact is established from the explorations—the ruins are of Pueblo origin. Of this there can be no question. The plan of the structure is only such as the Pueblo Indians could have devised and carried out. It is not the work of white men, either Spanish or French, though it is very probable that both the Spanish and French may have occupied this and other structures at this locality at later times, or even contemporaneously with the Pueblos. The finding of an iron ax, of rude and primitive workmanship, it is true, indicates white men's skill. It is very evident, also, that the metal instruments were used by the

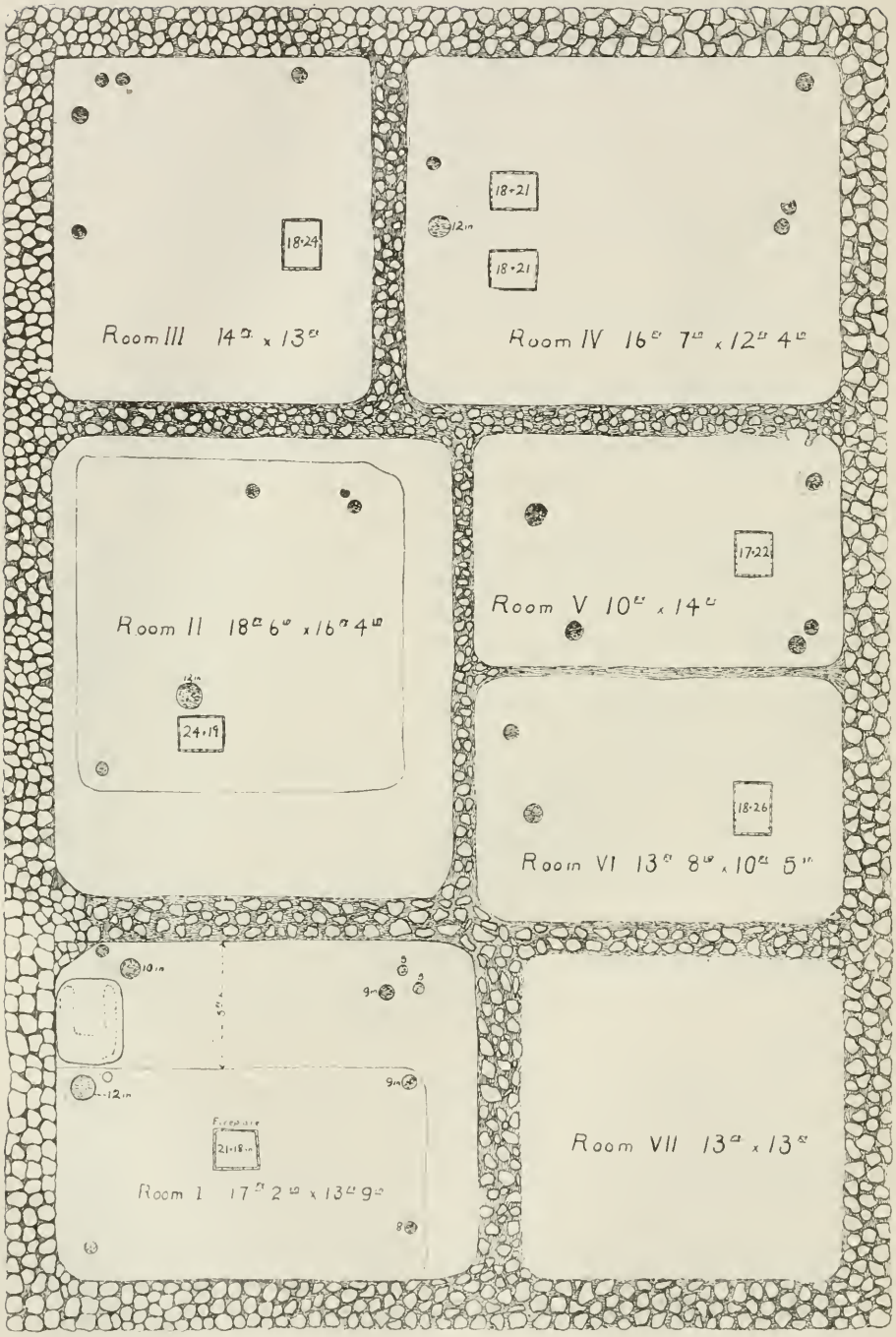
occupants. Several of the manufactured articles show clearly the imprints of metal saw teeth.

"The origin of the ruins is of course not positively proven, yet I believe that concerning this there is scarcely a doubt that they represent the old fortified place known as Quartelejo, founded about 1650 by a party of Indians who fled from the oppression of the Spaniards, from Taos, in New Mexico. The only information concerning this place that I have so far been able to obtain is from the works of Hubert Bancroft, volume 17, on Arizona and New Mexico."

The following is the full description of the ruins as published in the Kansas Historical Collections by the present writer:

"In the excavation of the chief structure referred to in the cited paper, all possible care was taken to avoid mutilating the plastering with which the walls were covered, thus permitting the exact size and shape of each room to be ascertained. As now excavated, the walls are about two and a half feet in height. The structure measures fifty by thirty-two feet in size, and stood as nearly due east and west in its greater measurements as it would be possible to locate it with an ordinary compass. The outer walls were of heavy stone, from eighteen inches to two feet in thickness, and were cemented or grouted together, making the full measurement of the building about fifty-three by thirty-five feet. The building site, as has been described by Doctor Williston, was a slightly raised mound, about seventy-five yards from the bed of Beaver creek, which here affords an abundance of water for both irrigational and domestic use. By the side of the building there are two large, hollowed out places, which had probably been used for the puddling and mixing of the adobe employed in the construction of the building. The stone used in the building, all of which had been brought from the surrounding hills, was considerable in amount, and many single pieces are all that a man can lift.

"About 100 yards south of the main edifice there is evidence of several other smaller buildings, all of which must have been constructed of adobe alone, since no rock remains. These smaller structures, two of which were examined by us, yielded no utensils or other relics; nor could their size and shape be made out with certainty. Both of these buildings, as well as the large one, present evidence of having been destroyed by fire, whether as the result of some accident or by Indian foes one


18·24
Room III 14ft x 13ft
18·21
12in
18·21
Room IV 16ft 7in x 12ft 4in
Room II 18ft 6in x 16ft 4in
24·19
17·22
Room V 10ft x 14ft
18·26
Room VI 13ft 8in x 10ft 5in
10in
9in
12in
9in
Fireplace
21·18in
Room I 17ft 2in x 13ft 9in
Room VII 13ft x 13ft

cannot say, of course. From the fact that no human bones were found anywhere about, the probability of design is lessened. That the larger structure had been destroyed by fire there can be no doubt, since the adobe is burnt, and charcoal is thickly scattered everywhere; the stone and bone implements also all show evidence of fire. Rooms IV and VII, as I have designated them, show only slight evidence of the fire, and it is possible that one or both of these rooms had never been covered, and hence contained but little subject to destruction by fire. Room IV had portions of the rotted posts, evidently used as a ladder, remaining.

"Charred corn was found in every room except VII, in some places four or five inches deep. In room V there had been four or five bushels of this corn in a slightly hollowed out place at one side.

"About twenty-five yards north of the main structure there appears to have been three or four small structures, each separated a small distance in an east and west line parallel with the main building. These structures were apparently circular in outline, and were perhaps teepes.

"The most interesting room in the structure is the one I will designate as room I. Its dimensions were seventeen feet by thirteen feet and nine inches. It had a raised dais or platform on two sides, about six inches high; that on the west side five feet and three inches wide; that on the north side two feet. The wider one was doubtless used for sleeping purposes, and the narrow one as a bench. Very near the center of the room there is a box-like receptacle, formed of thin stone set edgewise. Like the others described further on, the bottom of this one was about six inches below the level of the floor, and its size was eighteen by twenty-one inches. It had been plastered at the bottom, and contained, when examined, a quantity of clean wood ashes. The receptacle may have been for the grinding and mixing of corn. In the southwest corner of the room there is a peculiar structure three feet nine inches in length by two feet and one inch in width, inside measurements, built of adobe. Its walls are eighteen inches high at the west end and twelve at the east end, the slope gradual from one end to the other. The walls, five or six inches in thickness, had been nicely rounded at the top. In the middle, and joined to the west end, is a small platform, about sixteen inches in length by twelve in width, raised about six inches above the bottom

of the grooves which surround it. These grooves, shaped somewhat like a U, slope toward the closed end. This part was filled with ashes, suggesting that the use of the oven was for the baking of pottery. Near the east end was a large hole, twelve inches in diameter and eighteen inches in depth, covered with a flat rock. It contained nothing save fine dust.

"The walls and floors were nicely plastered. The plastering gave no indications of finger marks, but seemed to have been smoothed off with some instrument. Stones that might have answered such uses were found in the rooms. In this room was found a small pipe, decorated with horizontal markings. Here also were found a needle or awl for the sewing of hides, several arrow-heads, fragments of pottery, and bone needles. The remains of two posts, about eighteen inches apart, were found in the northeast corner, evidently for the uprights of a ladder for ingress and egress. Similar holes in like positions were found in the other rooms. There were no indications of doors or other openings in any of the rooms. The roof was evidently made of willow poles or brush covered with adobe, as large quantities of the latter show impressions of twigs.

"Room II was sixteen feet and four inches in width by eighteen feet six inches in length, and had both wall and floor plastered. The fireplace was two feet by one foot seven inches in size, and close by it was a hole twelve inches in diameter. On the east end there was a bench, as in room I, four feet two inches in width, and on the north side one two feet in width, while on the other two sides the width was but twelve inches, but raised to about ten inches in height. Close to the fireplace was found a grooved stone maul, ribs with marks of a saw upon them, arrow points, pottery, bone and stone scrapers, and a small pipe. On the ledge at the east end was found the half of an iron ax or wedge. The iron of course is much rusted, and the tool appears to have been split longitudinally and transversely by some mishap. It had a groove near the head, instead of an eye, for the attachment of the handle, after the manner of the stone axes of the aborigines. This room contained more charred corn than did any of the others.

"Room III was fourteen by thirteen feet in size, with plastered walls and floor, the corners rounded at the east end and square at the west. It had a fireplace eighteen inches by twenty-four, and a raised dais four feet wide at the west end. The holes for the posts supporting the roof and for the ladder

were as in the other rooms. The plastering turned up about the posts showed that this work had been done after the roof had been placed over the structure. This room furnished grinders and several bone implements—scrapers and fleshers —made from the shoulder-blade of the buffalo and deer and antelope. The wall posts were rotted in the ground, and not burnt as in the other rooms, nor were the bone implements partly burned, as was the case with those in the other rooms. In this room, also, was found part of a musical instrument, a flute or flageolet, made from the wing bone of a large bird; also a bone implement with a serrated edge.

"In room IV fewer implements were found than was to be expected, for few marks of fire were visible. Owing to this, the room was in better condition for articles to have been preserved. It is just possible that the fire started on the south side, giving the occupants a chance to save most of their belongings from this room. Several scrapers, knives, also the small arrow points on plate I, Nos. 1, 2, 4, 5 and 12, 16, 17, 18, 19, 20, all of which are fine examples of workmanship, were found.

"Room V was the smallest in the building, being only ten by fourteen feet in size. It had well-plastered walls and floor, a fireplace seventeen by twenty-two inches in size, a large quantity of corn, arrow-heads, grinders, scrapers, pottery, etc. Close by the fireplace there was a hole in the floor covered by a flat stone that had been undisturbed. At its bottom was found half of a clam shell, which had been sawed lengthwise with a toothed saw, the tooth marks being very plainly apparent. In the northwest corner was a small oven, nine inches in width and sixteen in depth, excavated from the wall of the room and plastered throughout. It contained three or four inches of wood ashes in the bottom. In this were also found three oval and one square adobe bricks, about ten by fourteen inches in size, flattened above and rounded below. They may have been used in the baking of tortillas.

"Room VI was ten feet five inches in width by thirteen feet and eight inches in length. The level floor had been plastered, as also the fireplace, which was eighteen by twenty-six inches in size. There was a narrow partition between this room and room V, and since no indications of a ladder were found here it is possible that the two rooms had been connected. Several

scrapers, of bone and flint, together with grinders, etc., were found here.

"Room VII, thirteen feet square, differed from all others in having no fireplace or plastered walls. Numerous bones of bison, deer, antelope, coyote, badger, etc., were discovered in this room. The only relics were bone and flint scrapers. Probably the room had been used as a sort of storehouse, and not for human dwelling.

"The pottery found was in part composed of plaster of Paris, possibly obtained from the crystals of selenite scattered over the chalk exposures in the vicinity. A number of ribs were found which had been smoothed at one end into a sort of spatula, and had probably been used in the making of pottery or in the plastering of the building. Coiled as well as smooth pottery was found, but only a single piece that showed evidence of decoration. Some of this pottery has been submitted to Professor Hewitt, of Las Vegas, N. M., who has given much attention to the work of the Pueblo Indians. He was of the opinion that all this pottery had been introduced from New Mexico, and had not been made in the vicinity of the building or village. Probably this is the furthest east that such pottery has yet been found. In one of the rooms were found several squash seeds; some between two pieces of pottery, in good condition, others much decayed."

In the above account by Doctor Williston, he very graphically described the locality, surroundings and natural resources in the immediate vicinity of the ruins, which he had visited in 1896, but unfortunately was unable then thoroughly to investigate. He also gave a number of important quotations from the works of Hubert Bancroft, an eminent writer on Arizona and New Mexico. These works treat largely of the early history of the Spanish in America, and contain important data relative to the position of the pueblo known as Quartelejo, and the condition under which this isolated post was first built and peopled. From the above-named works it appears that about 1650 a band of Taos Indians fled to the plains and fortified a place called Quartelejo. In the papers of the Archæological Institute of America, American series V, Hemenway Archæological Expedition, A. F. Bandelier, page 181, says: "In 1704 the Indians of the pueblo of the Picuries abandoned their village in northern New Mexico and fled to the plains, where they established themselves at a place called El Quar-

telejo. Superstition was, from all indications, the cause of this hasty movement." In a foot note he adds: "This flight of the Indians of the Picuries to the Quartelejo is mentioned in several documents. I quote here only the witchcraft trial, entitled '*Causa Criminal contra Geronimo Dirucaca, Indio del Pueblo de Picuris,*' 1713, MS., fol. 16, 17. The same document also fixes the date. In regard to the return from Quartelejo, it was effected in 1706 by Sargente Mayor Juan de Uribarri."

For some reason or other there appears to be a conflict as to the exact date of the settlement of the Indians at Quartelejo, yet both the above writers agree that the return to Mexico was effected in 1706. This would indicate clearly that both Bancroft and Bandelier were writing about the movements of one and the same band of Indians. Furthermore, it does not appear credible that the governor of New Spain would have allowed these discontented Indians to have stayed at Quartelejo from 1650 until 1704, a period extending over fifty years, without an effort being made to effect their return, and in all probability Bandelier's date of the founding of this isolated pueblo in 1704 is the more correct.

He further states that "in all probabilities the place got its name from the fact that these Picuries Indians made a temporary stay there." This is also intimated by Fray Silvestre Valez de Escalante in his letter to Father Agustin Morfi, April 2, 1778. After the evacuation of the pueblo in 1706 at the instance of Uribarri, another band of friendly Indians must have taken possession of and occupied the place for a number of years, for from Bandelier we learn that in 1719 Governor Don Antoni Valverde Cossio, having determined upon a campaign into the north and northeastern plains (a movement made chiefly against the Yutes and such of the Comanches as had joined them), penetrated as far as the Quartelejo, and even beyond. A part of Valverde's object was to secure the rancherias of the Jacarrilas against their foes. Part of these friendly Apaches lived at Jacarrila, forty leagues north of Santa Fe, and another band lived at Quartelejo. Again, we find that in the following year, 1720, Don Pedro de Villazur called at this pueblo on his ill-fated trip to the Pawnee village which is supposed to have been located on the Platte river, when all perished at the hands of the treacherous Indians. After this I have been unable to find the place mentioned by any other writers of early southwestern history. And it is

more than probable that after the Pawnees had annihilated Villazur and his soldiers they also, to check the inroads and settlement of the Spanish and their allies, destroyed the Quartelejo, thus effectually clearing the whole country north of the Arkansas river. This would admirably account for the entire pueblo and settlement being destroyed by fire, as it undoubtedly was. From the position of the utensils and implements found, a very hurried departure must have been made from the main structure. Most of the meal-grinding apparatus found in each room appeared to be left in a group, as though just laid aside after use. This, and the finding of so much charred corn in most of the rooms, would surely indicate that no prearranged plan of evacuation had been decided upon. That the ruins are those of the Quartelejo mentioned by the old Spanish writers, to which conclusion Doctor Williston came after seeing the group of relics obtained, there can be no doubt.

Dr. F. W. Hodge, of the Bureau of Ethnology, says, in the American Anthropologist, volume 2, October and December, 1900, that he regards the discovery of the ruins as of great interest, that they are of typical pueblo fashion, and, in conclusion, says: "The former existence of this pueblo has been known to students of southwestern history and ethnology for a number of years, but not until the publication of the results of the investigation had its situation been known, and there is no reasonable doubt that the identification is correct, for pueblo architecture is intrusive in Kansas."

If the identification by Doctor Williston as Quartelejo is correct, then the exact locality of this pueblo, so often referred to by the old Spanish writers, and to which Don Juan de Archuleta journeyed, is assured, and as such should be of great value in assisting to prove more definitely that the localities designated by Brower and Hodge as the site of Quivera and Harahey are correct, and thus have some bearing as to the probable line of march of Coronado, and help to prove that he did cross the Arkansas river.

Brower says, in his "Harahey," page 27, volume 2: "When the final acceptance shall have been established that Coronado reached and crossed the Arkansas river and followed its course to the great bend, then the true site of Quivira and Harahey will have been finally reached and comprehensively understood."

By referring to a quotation given by Doctor Williston in his

paper taken from the narrative of Fray Silvestie Velez de Escalante, April 2, 1778, translated "In the Land of Sunshine," we find that Don Archuleta found in the possession of the Indians of Quartelejo pieces of copper and tin, and that they said they had procured them from the Quivera pueblos, to which they had journeyed from Quartelejo.

If these Indians had visited Quivira as they claimed, and Quivira and Harahey was where Brower and Hodge have located it, northeast of Quartelejo, then the presence in the ruins of the sandstone arrow straighteners can be satisfactorily explained, and the possession of knives and arrow heads of the Harahey type and material does tend to prove they had communicated in some way with the Quivira settlement. The arrow straighteners referred to, and which were found in the ruins, are made of the Dakota Cretaceous sandstone.

The writer has found many arrow straighteners on the western Kansas prairie made by the plains Indians, within a few miles of the ruins, but these were all of a different and harder material. Dakota sandstone in any shape is intrusive in the neighborhood of the ruins, but a journey to Quivira by the Indians of the Quartelejo would take them directly through the outcroppings of Dakota sandstone which occur in Ellsworth, Barton and Rice counties, and enable them to procure and carry back with them this valuable acquisition.

In a previous paper the writer made mention of a peculiar U-shaped structure that looked like it might have been used for the baking of pottery, on the raised platform-like center piece, a photograph of which is shown on plate VI, fig. 3. This, Dr. F. W. Hodge, in the American Anthropologist of October and December, 1900, says is a typical pueblo grinding trough, and on the raised platform in the center was undoubtedly fixed the grinding stone.

The small fireplace and chimney built into the wall of room V is due to the influence of Spanish associations, for at this early date chimneys were unknown to the Pueblo Indians of New Mexico. The chimney leading to the roof was carried up the center of the wall between rooms V and VI, and was plastered inside, provision being made to allow for room for this by a thickening of the wall at this point. It is of course not known of what material the inner walls were composed, but from the amount of rock that had been removed from the ruins for building purposes by settlers the past twenty years,

and the amount remaining at the time of the excavations, I think it is safe to presume that the whole structure, with one exception, was composed of rock. The wall separating rooms V and VI was entirely too thin to allow of being built of stone, and was in all probability made of willows woven together and plastered over. The division wall extended clear across the room to a height of eighteen inches, and although no opening for communication showed at this height, it is more than possible that these two rooms were connected by some opening in the division wall higher up, considering the fact that in room VI no post holes remained showing any indications of their having had a ladder for communication with the roof.

It is much to be regretted that out of the vast amount of material that has been collected in and around the 100 or more village sites enumerated in Brower's Harahey, not more than a dozen specimens have been secured for the University collection of archæological material. Yet Brower states that more than 10,000 archæological specimens have been gathered, and are deposited in the museum of the State Historical Society of Minnesota.

As a means of advancing the study of the earliest history of the state, and as an inducement to students interested in archæology and ethnology, scarcely could there be anything more valuable and important than a well labeled, systematically arranged series of archæological specimens collected from these historical old village sites of Quivira and Harahey, visited so long ago by Coronado and his followers.

I here wish to convey my thanks to Dr. C. E. McClung for his assistance in the preparation of this paper, and for his kindly advice and corrections.

In the near future a model of these interesting ruins, the first ever inhabited by white man in the state of Kansas, will be constructed and placed in the University museum.

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CONTENTS:

THE INFLUENCE OF MAGNESIUM SULPHATE ON THE MOTOR CELLS OF THE CEREBRAL CORTEX, . . *H. F. Hyndman and W. E. Michener.*

PUBLISHED BY THE UNIVERSITY,

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THE INFLUENCE OF MAGNESIUM SULPHATE ON THE MOTOR CELLS OF THE CEREBRAL CORTEX.

BY H. F. HYNDMAN AND W. E. MICHENER.

(Contribution from the Physiological Laboratory of the University of Kansas.)

THE experiments of which the results are here briefly recorded were undertaken for the purpose of ascertaining whether magnesium sulphate paralyzed the motor cells of the cerebral cortex. It was found that 1.5 grams of magnesium sulphate per kilo, when injected in rabbits subcutaneously, produced anæsthesia in about fifty minutes that lasted two hours.

Rabbits were employed in all of the tests and three series of experiments were carried out.

In the first set ether was given, and when anæsthesia had developed the motor areas were exposed, and a definite, well-defined small area, which when stimulated with insulated platinum electrodes with a determined minimal strength of induced current, caused the hind leg of the side opposite to the one stimulated to give a definite contraction. The cortex was then carefully removed and again the minimal strength of current determined that would produce the same extent of contraction as before in the same leg. The animal was then allowed to come from under the influence of ether, and then an anæsthetic dose of magnesium sulphate was injected. The same area on the opposite side was now stimulated with a determined minimal strength of current that would produce the same extent of contraction as was secured with ether. The cortex was then removed and again the minimal strength of current determined.

The experiment was also modified in that the minimal

strength of current for contraction was determined after cortex stimulation, and then, when the animal recovered from the ether effect, magnesium sulphate anæsthesia was secured. Again the cortex was stimulated with a minimal strength of induced current.

The results of this set of experiments were that it required exactly the same strength of current to produce the same extent of contractions, both with the cortex intact as well as when the motor cells were removed and the fibers directly stimulated under ether as under magnesium sulphate anæsthesia. In each case the strength of current required for the same contraction was greater when the motor fibers were directly stimulated after the motor cells were removed than when the contractions were secured indirectly by direct stimulation of the motor cells.

The second set of experiments differed from the first set in that the same procedure was carried out under magnesium sulphate anæsthesia alone.

The third set of experiments consisted in determining the strength of current when applied to the central ends of the eighth and seventh cervical dorsal spinal nerves under ether and magnesium sulphate anæsthesia that would reflexly cause contraction of certain muscles of the mouth.

A comparison of all the experiments showed that the same minimal strength of current was required to produce the same extent of contraction under ether as under magnesium sulphate anæsthesia, whether applied directly to the motor fibers, indirectly to the fibers through the motor cortical cells, or when applied to afferent fibers that secured a reflex response; and that a greater strength of current was required when applied directly to the motor fibers than when the impulses reached these through stimulation of the motor cortical cells.

We conclude, therefore, that magnesium sulphate anæsthesia does not paralyze the motor cells of the cerebral cortex in the rabbit.

We take this opportunity to thank Doctor Hyde, under whose supervision these experiments were conducted, for her many kind suggestions.

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A Study of the Respiratory and Cardiac Activities and Blood Pressure in the Skate Following Intravenous Injections of Salt Solutions, ... *Ida H. Hyde.*

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A STUDY OF THE RESPIRATORY AND CARDIAC ACTIVITIES AND BLOOD PRESSURE IN THE SKATE FOLLOWING INTRAVENOUS INJECTIONS OF SALT SOLUTIONS.

BY IDA H. HYDE.

Plate X, and 49 figures.

(From the Marine Biological Laboratories of Woods Hole and Leland Stanford[1] and the Physiological Laboratory of the University of Kansas.)

THE experiments that are recorded in this article were conducted on the skate, *Raia erinacea* and *Raia binoculata*, during the summers of 1902, 1903, 1906 and 1907.

A host of articles have accumulated since Humboldt first studied the action of salt solutions upon the rhythmical changes in the heart's contractions; but with the progress of physical chemistry new problems and different views presented themselves and left many important questions still unsettled. To aid in solving some of these I undertook the study from a less general standpoint by employing a method and an animal seldom heretofore adopted in the solution of the questions. A few experiments were begun on the fresh-water sturgeon and on the frog in order to compare the results with those obtained with the skate. These, however, will be extended and varied before the results are published.

It was hoped that simultaneous records and comparisons of the three activities might throw some light upon the factors that influence them and indicate whether their nerve centers are alike stimulated by the same ions. At first the object was also to determine whether it was the anion or cathion that

1. I take this opportunity to express my hearty thanks to the directors for the privilege of working in these institutions and for the courtesies I received there.

stimulated the different centers, and if there were ions that simulated one but proved neutral or inhibitory to the other centers. Moreover, whether valency or solution tension were influential factors, and if the toxicity produced on either the respiratory, cardiac or vasomotor centers by certain salts could be counteracted by definite amounts of other salts that proved antitoxic. Before I had proceeded far, however, I desired, in addition to the solution of some of these questions, to study other physical and chemical effects that were produced in the body by the salts; *e. g.*, osmotic pressure, the products of chemical reactions, such as oxygen, carbon dioxide, hydrogen and hydroxyl ions, and the dosage of the solutions.

I realize that in experiments of this character a host of phenomena may exert their influence and that it is difficult with the data at hand to assign to any special one the cause that produces the particular result. Some of the events which may deserve consideration can, however, be controlled and their influence either accounted for or removed from further consideration. That is especially so in the investigation of the fishes, where the temperature and supply of the water can be controlled and are kept normal and constant throughout the experiment and where the amount of solution injected bears a direct proportion to the weight of the animal, and also where from the method employed mechanical stimulation, either due to the insertion of the cannula or brought about by retaining the fish in a definite position during the experiment, is avoided.

On the other hand, we assume that the addition of an isotonic salt solution to the blood, the chosen amount of which does not cause any change in any of the functions under consideration, will, if hypo- or hyper-tonic, produce various physical and chemical alterations both in the fluids and tissues of the body. Introducing an additional salt into the blood assumes changes in its osmotic pressure and in the contents of the corpuscles, also alterations in the permeability of the walls of the capillaries, corpuscles and other tissue cells. Or the new composition in blood salts may make new combinations with colloids or ferments or proferments, or set free ions that will thus stimulate or inhibit functions by acting directly on cardiac or muscle cells, or indirectly upon special centers. That is, the physiological property of the blood is altered by changing the proportion and character of the electrolytes in it, and this must have

its peculiar influence upon the life phenomena of respiration and heart action and blood pressure. To which of these must be ascribed the important changes produced in respiration and cardiac activity and blood pressure is a question with which I shall not for the present concern myself, since in addition to the experiments which I conducted it would be necessary, as I later saw, to carry on extensive physical and chemical investigations for which I lacked the time. I shall content myself, therefore, by simply stating my method and observations, and not attempt theoretical considerations of the underlying causes, trusting that the data obtained from over 200 experiments will aid in the correct interpretation of results secured by other investigators working upon problems related to those that I undertook.

According to Garry[2] and Sumner[3] the percentage of salts in the skate and selachian's blood does not differ from that in sea water. The lowering of the freezing point being —1.8° C. and the osmotic pressure twenty-two atmospheres, the sea water is therefore isotonic with the skate's blood, while Baglioni[3] estimated it isotonic with an m⅝ NaCl or a 2 per cent NaCl plus 2.5 per cent urea. Although the osmotic pressure of the selachian's blood is the same as sea water, its salt content is less, but the lowering of the freezing point is compensated by the urea in the blood.

Employing Welcker's method, I ascertained that a small skate weighing from 550 to 700 grams possessed 25 to 30 grams of blood, or about one-twentieth of the body weight. Harris[3] states that the weight of the blood in the skate is only one-fortieth of the body weight, but he does not describe the method employed for ascertaining his data.

Although there are wide variations in blood pressure, I found that the mean pressure for an average-sized skate was about 20 mm. of mercury.

The photograph on plate X illustrates one of the methods employed for securing records of the respiratory and cardiac action and blood pressure. The skate was placed ventral side up on an inclined board, partly submerged in water, and held in place by fish netting; a constant stream of fresh sea water

2. Garry, W. E. Biological Bulletin, 1905, vol. VIII, No. 4, p. 257.

3. Sumner, F. B. Bulletin Bureau of Fisheries, 1906, p. 596. Baglioni. Zentralblatt für Physiologie, 1905, vol. XIX, p. 12. Harris, D. F. Journal of Physiology, 1903, vol. XXX, Nos. 3 and 4, p. 319.

of a definite volume, velocity, and temperature entered the mouth through a forked glass tube covered with rubber tubing.

As soon as the water enters the mouth and flows out of the gill slits over the body, thus keeping the skate practically submerged, and the netting comes in contact with the body, the fish is perfectly quiet and remains so for hours, apparently contented and comfortable. A cannula, filled with 20 per cent glucose or glucose and 1 per cent ammonium oxalate, is inserted in one of the side branches of the aorta and joined to a delicate mercury manometer placed quite on a level with the blood vessels. To the open end of the manometer is attached a Hürthle manometer, which records the heart action, while the pressure is read off directly from the manometer.

By means of a silk loop one of the gill arches is attached to a light lever which records the respiratory movements. In control experiments the tip of the ventricle was exposed and by means of a silk loop joined to a light lever, so that in addition to the above records, separate ones were obtained of the rate and force of the heart's activity.

The salts employed in the experiments were all chemically pure, either from Kahlbaum or specially prepared in the laboratory, and they were all standardized. The water employed in making up the solutions was twice distilled in glass.

To avoid mechanical stimulation a cannula, to which was connected a rubber tube, was inserted either in the median or lateral caudal vein and tied in place. Subsequently 4 cc. of the solution per kilo weight of fish was slowly pressed from a graduated glass tube into the cannula by means of a rubber bulb attached to its upper end.

During the inspiratory phase the mouth and spiracles are opened, the floor of the mouth is lowered, the gill clefts or external branchial apertures are closed, and water enters the mouth and spiracles. In the expiratory phase the mouth and spiracles close, the floor of the mouth returns to its normal position or is elevated and the gill clefts open to allow the water to escape. Occasionally a peculiar spouting takes place during which water is thrown from the mouth and spiracles. This is observed in the aquarium also and may be due to irritation, touch, stimulation of the mucous lining of the mouth by slime particles or vitiated water.

I first investigated the effect of different concentrations of

the same solution, seeking the weakest solution that produced any change in the three functions under consideration; also, which concentration proved toxic, and whether the injurious dose could be modified or antagonized by a definite dose of another salt.

Observations were made and curves secured before, during and after the injection of the salt solutions. From one to five minutes after the injection a change in one or more of the functions under consideration usually occurred, and this was followed by a second change that lasted from five to twenty minutes, before the records again assumed their normal character. The first effect may be the reaction of the salt upon the constituents of the blood and indirectly upon muscle and nerve cells; the second is due to osmotic pressure changes. That injections of hypertonic salt solutions in the blood of the dog increases the osmotic pressure, which may become normal within twenty minutes, was proved by Magnus.[4] Moreover, those salts that set free O, CO_2, H, or OH ions, in their reactions. exert their influence more often through these ions, and effect results that differ from those produced by salts having the same cations, but do not react with the same resulting ion products; *e. g.*, NaCl is different in its effects from Na_2CO_3, probably because of the OH ions set free by the Na_2CO_3 dissociation.

It is possible that the blood pressure, respiratory and cardiac activities depend upon the number of molecules and ions in the blood, and upon the dissociation tension of the salts. The prepotent anions or cations may stimulate or inhibit enzyme action, and thus aid in producing the inner stimulus that affects alike the force of cardiac and respiratory activity and directly or indirectly the blood pressure.

A careful study of very many experiments with the same salts was made, the average results summed up, and the most typical of a series of experiments put in tabular form. Thus table II gives a survey of the different series of experiments and is a summary of all the experiments conducted on the skate with NaCl solutions. It shows that m/32, m/16, m/8, NaCl solutions produce as a rule practically no change in the heart or respiratory activity or blood pressure. An m⅝ NaCl solu-

4. Magnus. Archiv für Experimentelle Pathologie, 1900, vol. 44, p. 99.

tion (see curve 1) increases the force and blood pressure but leaves the rate of the heart and respiration unaltered.

An m/1 solution (curve 2) causes a rise in blood pressure and force of heart's rhythm at once, which usually continues for about twenty minutes. But the force and rate of respiration is either unchanged for one to two minutes and then decreases; or may, as does the heart rate, first decrease and then return to normal.

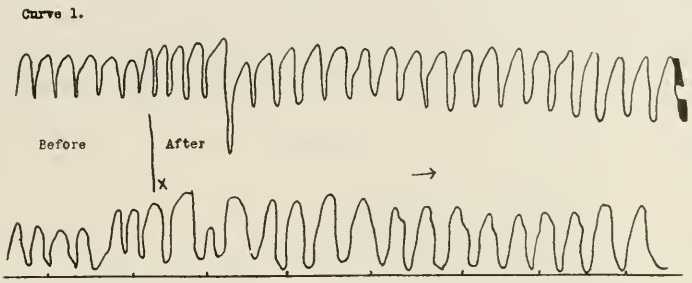
Following the injection of a 2m NaCl solution (curves 3 and 4) the blood pressure increased for about five minutes, then became normal. The rate and force of the heart and respiratory movements decreased for one to twenty-five minutes; but in many cases the force of the heart's activity first decreased for one to two minutes and then increased, or increased as the blood pressure rose. In every instance the systole and inspiratory phases were prolonged above normal with a 2m NaCl solution.

A *résumé* of the NaCl experiments shows that injections of 4 cc. per kilo fish of m/64 to m/8 solutions are as a rule practically indifferent; m⅝ stimulates the force of heart and respiratory activity and raises blood pressure for from one to five minutes, but is usually indifferent to rate; m/1 increases the force of the heart's action and also blood pressure, but the rate and force of respiratory activity differs in that they may for one minute remain normal, then decrease; or may, as does the heart rate, decrease for one to three minutes before resuming again the normal activity; 2m decreases rate and force of heart and respiration, but the heart's force is often increased after one to two minutes' decreased action. The blood pressure is raised during the first one to five minutes, then falls.

It might be concluded that the blood salts can be slightly increased by 4 cc. per kilo m/64 to m/8 without stimulating or inhibiting either of the three functions that are considered, and that equilibrium of the osmotic pressure is rapidly established. On the other hand, m⅝ stimulates the force of both heart and respiration. I infer that its effect is directly upon the nerve centers for one to five minutes, before the attraction of water to the blood establishes equilibrium. An increase to m/1 has a stimulating effect only upon the force of the cardiac center, thereby increasing also the blood pressure, but

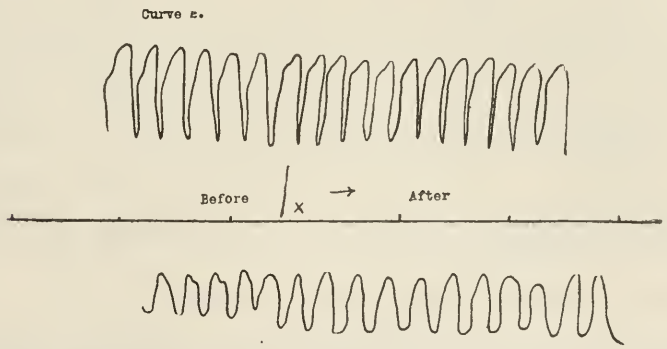
strangely enough does not affect the respiratory center in the same direction but rather depresses its force and rate, as well as the rate of the heart's activity. But a 2m solution has again a like depressing influence upon both force and rate of respiratory and cardiac rhythm and at first causes a rise in blood pressure.

CURVE 1. Following an injection of m⅝ NaCl. Lever attached to heart and gill arch.



Upper, respiration. Lower, cardiac curve. Injection at X. Force of heart and respiratory action increased, but not rate.

CURVE 2. After NaCl. Lever attached to heart and gill arch. Normal before X.



Upper, respiration. Lower, cardiac curve. Heart and respiratory rate unchanged; force of former increased but of latter unchanged or even less. Time, five seconds.

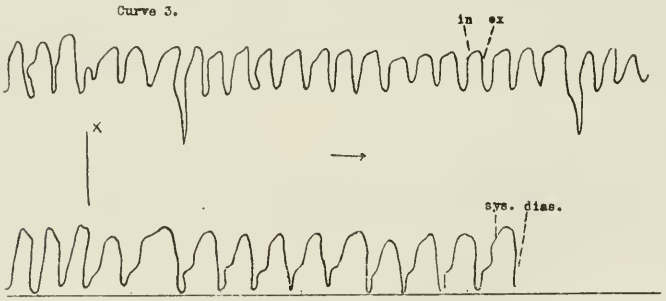
Data of the mean results in respiration, heart action and blood pressure of many experiments on the skate. Different

concentrations of NaCl were intravenously injected in the proportion of 4 cc. per kilo fish:

TABLE I. Effect of NaCl solutions.

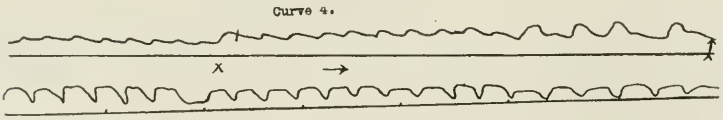
Salt amt.	Mol.	Heart rate.	Heart force.	Respiratory rate.	Respiratory force.	Blood pressure.		Time of change.	Curves.
						Normal.	Change		
NaCl 2 cc.	m/32	Neutral.	Neutral.	Neutral.	Neutral.	24	24		
NaCl 2 cc.	m/16	Neutral.	Neutral.	Neutral.	Neutral.	20	20		
NaCl 2 cc.	m/8	Neutral.	Neutral.	Neutral.	Neutral.	14	14		
NaCl 2 cc.	m/4	Neutral.	Increased.	Neutral.	Increased.	26	28	First 1–5 minutes.	1
NaCl 2 cc.	m/1	Fell 1–3 minutes, then normal.	Increased at once.	Normal or less.	Normal or less.	17	20	During 20 minutes.	2
NaCl 2 cc.	2m	Fell 36–30; systole prolonged.	First 1–2 minutes rose, then decreased.	First 5 min. fell, inspiration prolonged.	Decreased.	20	23	First 5 minutes.	3, 4

CURVE 3. After 2m NaCl. Heart directly attached to lever.



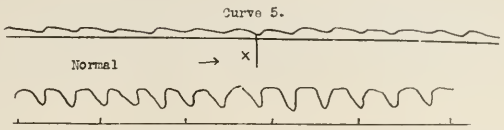
Upper, respiration. Lower, heart. Time, five seconds. Systole and inspiration much prolonged.

CURVE 4. 2m NaCl. Hürthle mercury manometer.



Normal, 10:35 A. M.	10:40 A. M.	10:45 A. M.
Heart rate, 36.	Heart rate, force slightly increased.	Heart rate, 30, force increased.
Respiration rate, 36.	Respiration rate 27, force slightly decreased.	Respiration rate 36, force less.
Pressure, 20.	Pressure, 23.	Pressure, 23.

CURVE 5. M/32 KCl. Heart and blood pressure were obtained with Hürthle manometer. For respiratory records the lever was attached to the gill arch.

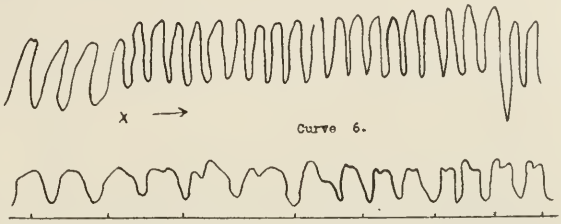


The upper curve heart, and from abscissa to heart blood-pressure record.

Below the latter respiratory curves, and the time in five seconds.

Blood pressure remained unchanged, respiratory rate decreased, force unaltered, expiratory phase prolonged. Heart rate from 24 to 22, prolonged diastole and force unchanged.

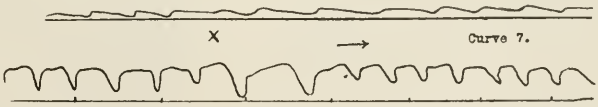
CURVE 6. M/8 KCl. Lever attached to the tip of the ventricle and gill arch.



Upper, respiratory curve. Lower, heart. Time in five seconds.

The first part of the upper curve of respiration, taken before injection, registered 36; immediately after, force slightly less, but the rate increased to 42, and in ten minutes was normal again. The first part of the lower heart curve before injecting was 34 per minute. For about twenty minutes it was less (27), with prolonged diastole, then gradually increasing during fifteen minutes to normal. Force was unchanged.

CURVE 7. Effect of m/8 KCl.

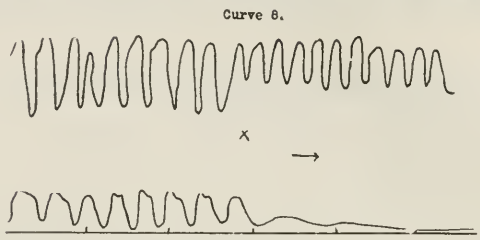


Upper, heart and pressure recorded with Hürthle mercury manometer.

Lower, respiratory records from lever attached to a gill arch.

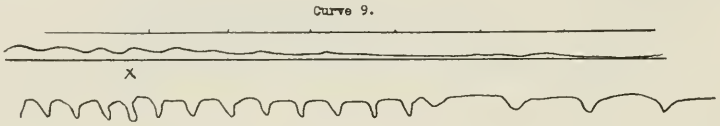
Pressure before injecting m/8 KCl 20 mm.; after injecting for two minutes 22 mm., then normal. After injecting the solution, the respiration for about twenty seconds decreased in rate with prolonged inspiration, then for about one minute increased, and in fifteen minutes was normal. Force was unchanged for twenty to sixty seconds, heart rate decreased with prolonged diastole, then in five minutes normal; force unchanged.

CURVE 8. M5/8 KCl. Curves secured with heart and respiratory levers.



Upper, respiration. Lower, heart curve.
Within one to two minutes after the m5/8 KCl was injected, the heart action ceased. Respiratory force decreased, rate increased, and stopped in twelve minutes.

CURVE 9. m5/8 KCl. Curves secured with lever and Hürthle manometer.



The upper are cardiac, the lower are respiratory records. Time, five seconds.
Within one minute blood pressure and heart action were zero. Respiratory rhythm decreased and in twenty minutes stopped.

TABLE II. Mean results in respiration, heart action and blood pressure following injection of different concentrations of KCl solutions.

Salt mol. 4 cc. per kilo.	Heart rate.	Time.	Heart force.	Respiratory rate.	Time.	Respiratory force.	Blood pressure.		Curves.
							Normal.	Change	
KCl m/100	Neutral.		Unchanged.	Unchanged.		Unchanged.	18	18	
KCl m/32	Slower.	20–60 sec.	Unchanged.	Increase, then less, or less at once.	20–60 sec.	Decreased or unchanged.	18 20	18 20	5
KCl m/8	Decreased.	20–60 sec.	Unchanged.	Decreased.	At once.	Unchanged.	20 20	18, 22, then 20	6 7
KCl m5/4	Decreased, then ceased.	5 sec.	Increased for 30 sec. then less.	Increased, stopped or decreased.	5 sec.; 7 min.	Decreased.	19 or 20	22, 1 min. 0, in 3 min.	8 9

The influence of KCl injections are summarized in table II, which represents the mean results of many experiments of the different series of KCl solutions. Curve 5 is a typical curve secured after injecting the usual amount of an m/32 KCl solution. From the table and the curve it is observed that an m/32

KCl solution produces a first effect of from twenty seconds to one minute upon the heart and respiratory activities. More often during this time the heart rate is slower, due to prolonged diastole, and the force remains unchanged. The inspiratory phase is, however, lessened while the expiratory is relatively prolonged.

Curves 6 and 7 represent records obtained with different methods after injecting an m/8 KCl solution. Although many other records were made these were chosen because they represent the more general type. There were exceptions in every case, but those variations were accounted for either because of the morbid condition of the skate, because it had been in the aquarium several days, or had been under observation for several hours and was fatigued or more or less irritable. After the solution was injected for from twenty to sixty seconds the heart activity greatly decreased and diastole was much prolonged. Occasionally the action increased above the normal rate for one to two minutes, and in ten to fifteen minutes was normal. The force remained unchanged. The respiratory rate as a rule decreased for fifteen to thirty seconds, with prolonged inspiratory phase, then either suddenly increased above normal or gradually returned to the normal rhythm. The force was usually unchanged. The blood pressure either fell or increased slightly, about 2 mm. mercury, for from one to two minutes.

Following the injection of m⅝ KCl, pressure fell either very suddenly to zero or in rapid leaps from 20 to 16 in one minute and zero in two minutes, or often 19 to 22 in one minute then zero within three minutes. The heart decreased in rate; *e. g.*, from 30 to 18, with increased force in one and zero in two minutes. Respiration slowed from 39 to 30 in five seconds to 18 and very shallow and often irregular and spasmodic in ten minutes, or rapid, 46 to 60, in five seconds, and gradually to zero in seven minutes, but in some cases continued active as long as twenty minutes after the heart had ceased contracting.

A *résumé* of the effects of KCl solutions brings to light that diastole and inspiratory phases are prolonged above normal in the different strengths of solution. Blood pressure falls in all but the most dilute solutions. The force of the heart and respiratory activity is practically unchanged in all but the toxic strength, m⅝, after which it decreases. The rate of the heart's

contractions as a rule is at first decreased in all strengths but the m/100; m⅝ is toxic to heart and respiratory activity, though usually the respiratory rhythm continues for five to twenty minutes after the heart has ceased.

A summary of some experiments that were undertaken to study what salts counteracted the toxic influence of KCl solutions is shown in table II*b*, and curves 10, 11, 12 and 13 illustrate a few of the experiments.

Curve 10 records the antitoxic effect of an m⅝ NaCl solution. The rate of the heart's action was 36, that of the respiratory 26. At 10:05 m⅝ KCl was injected; within a few seconds the heart action became irregular and respiration rapid, then irregular, with prolonged expiratory phases. Blood pressure fell. At 10:15, an injection of m⅝ NaCl was followed in a few seconds by regular and strong cardiac and respiratory contractions, which in ten minutes were quite normal, but the force of the heart-beat was stronger. In other experiments the toxic effect of an m⅜ KCl was quickly counteracted by an m/8 NaCl solution.

Curve 11 shows the favorable influence of $CaCl_2$ with or preceding a KCl solution; m/4 KCl following m/4 KCl+m/32 $CaCl_2$ shows a decrease in force of heart and respiratory activity, and a toxic m⅝ KCl following a mixture of m⅝ KCl+ m/32 $CaCl_2$ shows, in addition to a decrease in rate, a marked decrease in force, but in twenty minutes the heart and respiratory rhythm is almost normal. The $CaCl_2$ evidently proved antitoxic, and with KCl enhances the force of both respiratory and cardiac action.

Curve 12 also shows that a dose of m/4 $CaCl_2$ that preceded an m⅝ KCl and m 1 KCl counteracted their toxic effects.

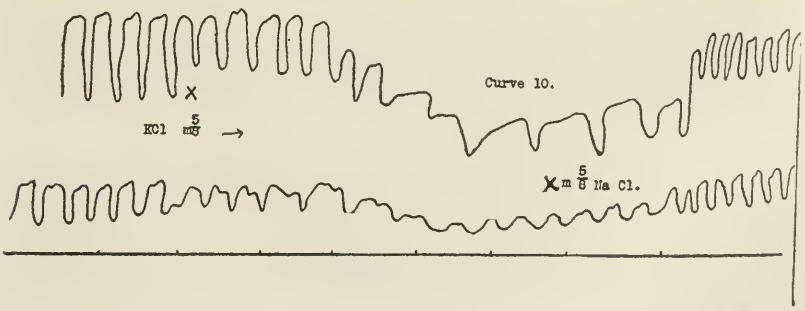
Curve 13: After $CaCl_2$ m⅛, blood pressure stood at 14 mm., heart action at 24, respiratory action at 36. When m⅝ KCl was injected, pressure fell to 2 mm, heart to four contractions and respiration increased to 42. At the end of two minutes pressure was again 14, heart and respiratory rate had increased, though shallow. At the end of five minutes, pressure and action of heart and respiration were quite normal, but respiratory rate more rapid. This shows that when stronger solutions of Ca are injected, and the blood is in excess of the normal, it counteracts the toxic effect of m⅝ solution of KCl quicker and the toxicity is less marked on respiratory than

heart action. In some experiments the toxic effect of KCl m⅝ was overcome if $CaCl_2$ was injected soon after the KCl solution.

TABLE IIb. Salts that counteracted the toxic effect of m⅝ KCl.

Salt amt.	Mol.	Heart.	Respiratory.	Blood pressure.	Antitoxic.	Mol.	Heart.	Respiratory.	Blood pressure.	Curves.
4 cc. KCl. per kilo.	m⅝	Irregular, then spasmodic.	Rapid, then spasmodic.	Pressure fell.	$NaCl_2$ cc. followed m⅝ KCl.	m⅝	Regular in two minutes.	Regular in two minutes.	Rose.	10
KCl	m/4 subsequent.	Rate unchanged, force less.	Rate increased, force less.		$CaCl_2$ + KCl. Preceded.	m/32 m/4	Rate unchanged, force increased.	Rate less, force increased.		11
KCl	m⅝ subsequent.	Rate and force less.	Rate and force less.		CaCl + KCl. Preceded.	m/32 m⅝	Rate and force increased.	Rate and force increased.		11
KCl KCl	m⅝ m/1	Slight increase in rate and force Unchanged.	Rate slight increased, force less.		$CaCl_2$. Preceded.	m/4	Stimulant force and rate antitoxic.	Stimulant force and rate antitoxic.	Rose.	12
KCl	m⅝ subsequent.	Almost stopped; in five minutes quite normal.	Rate increased, force fell, then normal.	Fell.	$CaCl_2$. Preceded m⅝ KCl.	m⅛	24	36	Normal.	13

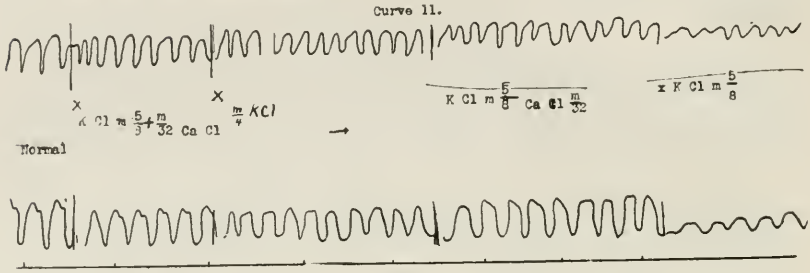
CURVE 10. Toxic action of KCl m⅝ counteracted by NaCl m⅝. Levers attached to ventricle and gill arch.



Time, five seconds. Upper, respiration. Lower, cardiac curves.[5]

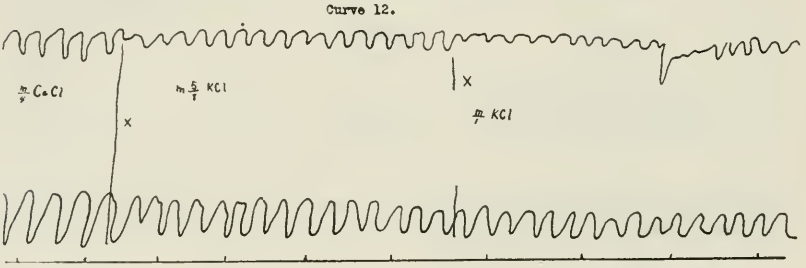
5. Within a few seconds after injecting m⅝ at X, the heart action became irregular and spasmodic in long diastole. In twenty-five seconds the greatly increased respiratory movements assumed prolonged expiratory spasms and a few seconds following m⅝ NaCl injection both respiratory and cardiac action became more regular again. m⅝ NaCl proved antitoxic for the toxic dose of m⅝ KCl.

CURVE 11. Toxic effect of KCl m⅝ counteracted by $CaCl_2$ m/32 for the upper curve. For lower curve, the lever was attached to the ventricle, and to the gill arch for upper.



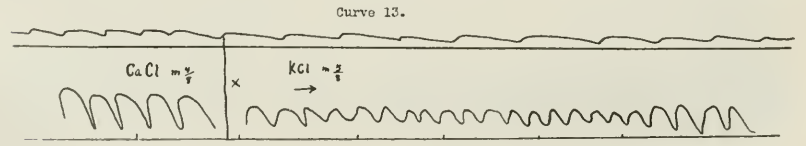
Showing the antitoxic and stimulating action of $CaCl_2$ 2 cc. m/4 KCl+ m/32 $CaCl_2$. Rate of heart contractions increased. KCl m/4 decreased the force of heart and respiration, while rate of respiration increased. The difference between the effect of m⅝ KCl and KCl m⅝ plus $CaCl_2$ m/32 demonstrates that $CaCl_2$ increases force of heart and respiration.

CURVE 12. Toxic effect of KCl m⅝ or m/1 counteracted by a previous dose of $CaCl_2$ m/4. For lower record the lever was attached to the ventricle, and to the gill arch for the upper curve.



Following 8 cc. of gradually increasing to m/4 doses of $CaCl_2$ the heart became distended and contracted more forcibly, due to the intracardiac pressure; m⅝ KCl injected increased the rate of cardiac and respiratory activity and an m/1 KCl injected ten minutes later failed to produce its usual toxic effect.

CURVE 13. KCl m⅝ following m⅛ $CaCl_2$. After m⅛ $CaCl_2$ was injected the pressure stood 14 mm., heart rate 24 and respiratory 36. At 3:50 P. M. KCl m⅝ was injected. In one minute pressure fell to 2 mm., heart rate to 4 and respiratory rate increased to 42. At the end of two minutes pressure stood 14, heart force increased rate 8, respiratory rate 48, force less. At the end of five minutes pressure and heart action were quite normal while respiration was abnormal in rate but normal in force.



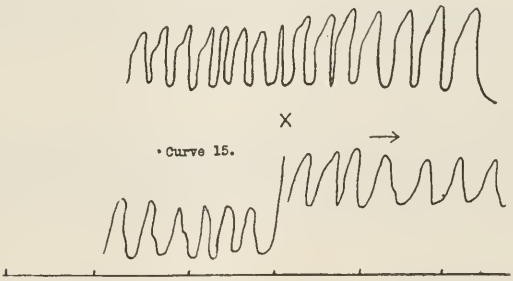
Upper curve, heart and pressure from abscissa. Lower curves, respiration. Time, five seconds. Records with Hürthle and lever manometer.

The results of the experiments with $CaCl_2$ are briefly tabulated in table III and partly shown in curves. It was observed that after an injection of the usual amount of m/32 $CaCl_2$ solution (curves 15, 16), the blood pressure remained unchanged. Respiratory activity was usually increased for one to three minutes, and the cardiac contractions continued unchanged or did so after about one minute of decreased rate and increased force. Following an injection of an m/8 $CaCl_2$ solution, the rate of cardiac and respiratory activity is usually decreased and the force of both increased. The blood pressure rises for about one minute. Often systole and inspiratory phases predominate, and furthermore, the solution proved antitoxic to many toxic salt solutions. The effect of an m5/8 $CaCl_2$ was first a decrease in rate of cardiac and respiratory activity, often irregular, with prolonged systole and inspiratory phases. The force of both activities was usually increased, as was also the blood pressure, for from one to three minutes. If the force of the heart-beat was not increased the blood pressure did not rise above normal.

TABLE III. Mean results in respiration, heart action and blood pressure, following injections of different concentrations of $CaCl_2$ solutions.

Salt mol.	Heart rate.	Heart force.	Duration.	Respiratory rate.	Respiratory force.	Duration.	Pressure.		Curves.
							Normal.	Change	
$CaCl_2$ m 32	Unchanged or decreased.	Unchanged or increased.	1 min.	Unchanged or increased.	Unchanged or increased.	3 min.	20	20	15, 16
$CaCl_2$ m 8	Decreased or unchanged.	Increased or unchanged.	1-3 min.	Unchanged or decreased.	Unchanged or increased.	1-3 min.	17	18	17, 18
$CaCl_2$ m5/8	Decreased or irregular.	Increased.	1-3 min.	Decreased or irregular.	Increased.	1-3 min.	22	24, 22	19, 20

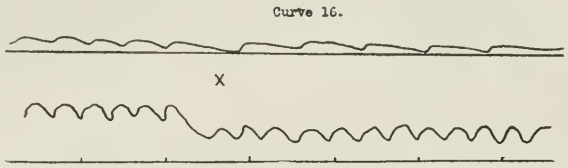
CURVE 15. Following an injection of m/32 $CaCl_2$.



Rate less and force of heart unchanged; rate of respiratory activity decreased for one minute, then normal, force increased.

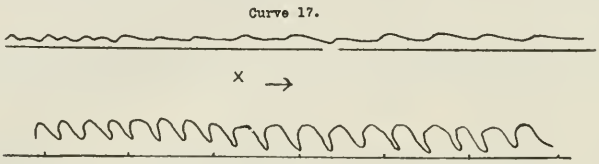
The upper respiratory and the lower cardiac records were secured with levers directly attached to gill arch and apex of heart.

CURVE 16. After m/32 $CaCl_2$.



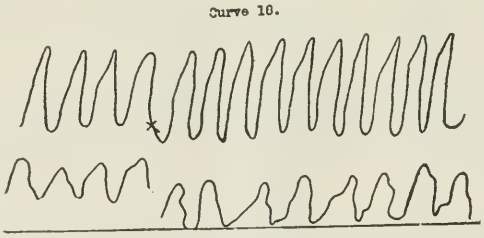
The upper curve, Hürthle manometer heart record. Lower curve, gill-arch lever records of respiratory activity. Rate of heart decreased, force unchanged. Respiratory activity and pressure unchanged.

CURVE 17. Effect of m/8 $CaCl_2$.



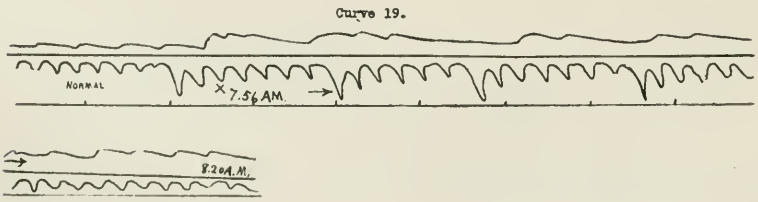
The upper curve is a record of the cardiac and blood-pressure changes secured with a Hürthle manometer. The lower respiratory is a gill-arch lever record. Rate decreased, force increased for both activities and blood pressure showed slight rise for a minute or two.

CURVE 18. Effect of m/8 $CaCl_2$.



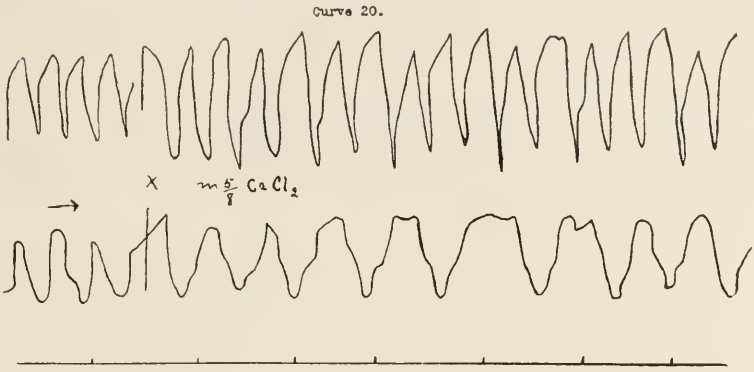
Upper, cardiac record secured with lever attached to the heart. Lower, gill-arch record. Respiratory rate unchanged, force increased. Cardiac rate decreased, force increased.

CURVE 19. Effect of m/8 $CaCl_2$.



Hürthle cardiac records above, gill-arch lever records below. Time, five seconds. Cardiac and respiratory rate decreased, force and blood pressure increased for about three minutes, then quite normal for about thirty minutes. First effect often irregular and spasmodic, especially for cardiac rhythm.

CURVE 20. Effect of m⅝ $CaCl_2$.



Upper curve respiratory, lower cardiac. Levers directly attached to heart and gill arch. Cardiac and respiratory rates first decreased, force increased; irregular prolonged diastole and inspiratory phases.

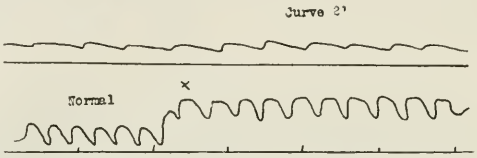
The results following injections of $MgSO_4$ solutions are summarized in table IV, and illustrated in the curves. It was observed that an m/64 or m/8 $MgSO_4$ had a more depressing influence on respiration than on cardiac activity. The rate was either unchanged or less, but force and blood pressure usually slightly greater for cardiac, while rate and force of respiratory activity were generally decreased.

An m⅝ or m/1 solution produces for about two minutes an increase in blood pressure followed by a decrease. Respiratory and cardiac rate and force both decrease, but occasionally the force of the heart's activity is first increased. Sensory reflexes are all reduced. With every strength of the solution the force and rate of the respiratory rhythm and the cardiac rate were decreased, but blood pressure and cardiac force were increased or decreased after a previous increase. With strong solutions, *e. g.*, m/1, diastole and expiratory phases predominated and the activities may become irregular, but an m/8 $CaCl_2$ overcomes the toxic effect and increases the force of the respiratory phase and blood pressure.

TABLE IV. Mean results in cardiac and respiratory activity and blood pressure following injection of different concentrations of $MgSO_4$.

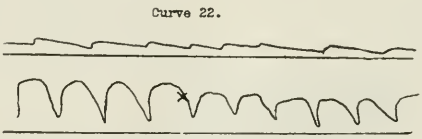
Salt mol.	Heart rate.	Heart force.	Duration.	Respiratory rate.	Respiratory force.	Duration.	Pressure.	Pressure change.	Curves.
$MgSO_4$ m 64	Less or unchanged.	Unchanged or increased.	15 min.	Less or unchanged.	Less.	15 min.	20	21 20	21
$MgSO_4$ m 8	Less or unchanged.	Increased or unchanged.	5 min.	Less or unchanged.	Less.	5 min.	18	19 18	22
m5 8 or m/1	Less or unchanged.	Decreased after rise.	Rise 2 m.	Less.	Less.	3 min.	22	23 21	23

CURVE 21. Effect of $MgSO_4$ m/64.



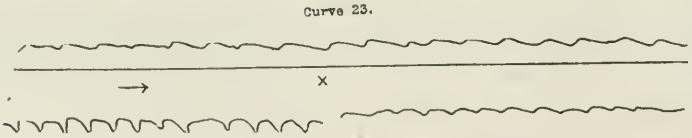
Upper curves, cardiac and pressure with Hürthle. Lower, respiratory gill-arch lever. Time, five seconds. At x, injection. Cardiac rate less, force and blood pressure slightly greater; respiratory rate less, force unchanged.

CURVE 22. Effect of $MgSO_4$ m/8.



Upper curve, cardiac and blood pressure shows decrease in cardiac rate, slight increase in force and blood pressure, for two minutes. Lower, respiratory gill-arch lever curve; decrease in force, not in rate.

CURVE 23. Effect of $MgSO_4$ m⅝.



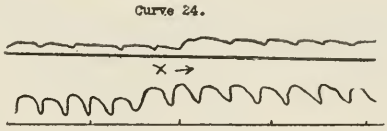
Upper curves, cardiac and blood pressure; rate unchanged, force and blood pressure slightly increase for two minutes, then decrease. Lower, respiratory curve, decrease in rate and force.

The effects of Na_2CO_3 injections are tabulated in table V. It was observed that Na_2CO_3 solutions are most effective in strengthening the force of the cardiac rhythm and thus raising the blood pressure. They do not stimulate respiratory activity except in strong doses, when they may increase the force. Its pronounced influence upon the heart may be due to OH ions that are set free by the dissociation.

TABLE V. *Résumé* of Na_2CO_3 injections upon cardiac and respiratory activity and blood pressure.

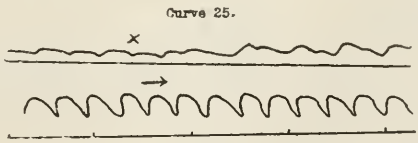
Salt.	Heart rate.	Heart force.	Duration.	Respiratory rate.	Respiratory force.	Duration.	Pressure.	Pressure changes.	Curves.
Na_2CO_3 m/32	Unchanged.	Increased.	15 min.	Unchanged.	Unchanged.		22	24	24
m/8	Unchanged or less.	Increased.	15 min.	Unchanged.	Unchanged.		20	23	25
m/16	Unchanged or less.	Increased.	2 min.	Unchanged or decreased.	Increased.		26	28	26

CURVE 24. Effect of Na_2CO_3 m/32.



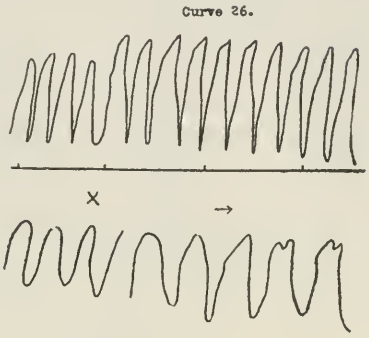
Upper curves, cardiac and blood pressure with Hürthle. Rate unchanged, force and blood pressure increased. Lower, respiratory; force and rate unchanged. Time, five seconds.

CURVE 25. Na_2CO_3 m/8.



Upper curves, cardiac and blood pressure. Rate decreased, force greatly increased, pressure rose. Lower curve, respiratory; force and rate unchanged. Time, five seconds.

CURVE 26. Na_2CO_3 m/2.



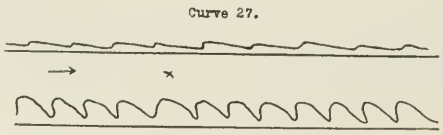
Upper, respiratory gill-arch lever records. Increased force, decreased rate. Lower, cardiac lever directly attached to heart. Increased force, decreased rate. Time, five seconds.

Na_2HPO_4 solutions are not so stimulating to cardiac rhythm as are Na_2CO_3 solutions. This is shown in table VI. Moreover, for the same strength they are more toxic. The solutions act like Na_2CO_3 chiefly upon the force of the cardiac action and are indifferent in weak solutions on respiratory movements.

TABLE VI. A summary of experiments of intravenous injections of Na_2HPO_4 relating to cardiac and respiratory activity and blood pressure.

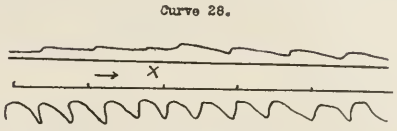
Mol. sol.	Heart rate.	Heart force.	Duration.	Respiratory rate.	Respiratory force.	Duration.	Pressure.	Change.	Curves.
Na_2HPO_4 m/64	Less or unchanged.	Increased or unchanged.	5 min.	Unchanged.	Decreased.	5 min.	23	24	27
m/8	Less or unchanged.	Increased or unchanged.	5 min.	Increased or unchanged.	Decreased.	5 min.	24	22	28
m/4	Less, then rapid or stopped.	Less.	5 min.	Less, then rapid.	Decreased.	3 min.	23	18	29

CURVE 27. Effect of Na_2HPO_4 m/64.



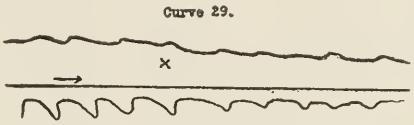
Upper, cardiac and blood-pressure Hürthle manometer curves; show force of heart action and blood pressure; slight increase, rate decrease. Lower, respiratory rhythm unaltered. Time, 5 seconds.

CURVE 28. Effect of Na_2HPO_4 m/8.



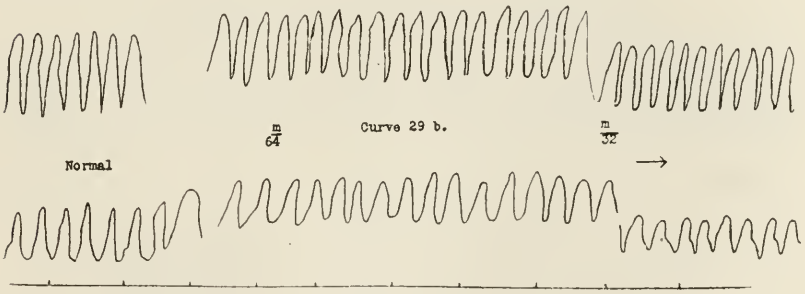
Upper, cardiac and blood-pressure Hürthle manometer curves. Rate little less, force slight increase. Lower, respiratory record; shows rate unchanged, force decreased, pressure decreased.

CURVE 29. Na_2HPO_4 m/4.



Upper, cardiac and blood-pressure Hürthle curves; show fall in blood pressure and for three minutes almost cessation of cardiac action. Lower, respiratory, force much decreased.

CURVE 29*b*. Effect of gradually increasing strength of Na_2HPO_4 solutions.



Upper, respiratory gill-arch lever curves show that with increasing strengths from m/64, m/32, m/8, m/4, solutions that the rate increased and force decreased from the normal and that this solution is more favorable to respiration as stimulating rate. Lower, cardiac apex lever curve shows that the rate remained practically unchanged except in m/4, when it became rapid and force decreased gradually from the normal.

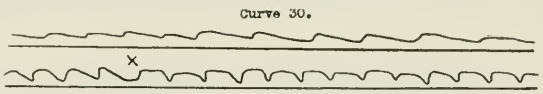
The influence of NaOH solutions is briefly tabulated in table VII. It is demonstrated that it acts, augmenting in all concentrations, on the force of the heart-beat and has not the same but rather a depressing effect on the respiratory center. The OH ions here, as in the Na_2CO_3, are the stimulating factors, but act more powerfully than in Na_2CO_3 solutions. The

respiratory force decreases with increased strength of the solution, while the blood pressure rises in all concentrations employed, showing that increase in blood pressure is not necessarily associated with rise of respiratory activity but rather with force of heart-beat.

TABLE VII Showing the effect of NaOH solutions upon respiratory, cardiac and blood-pressure changes.

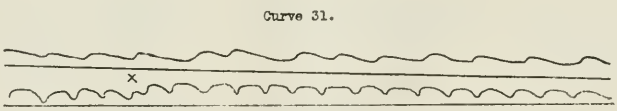
Salt mol.	Heart rate	Heart force.	Duration.	Respiratory rate.	Respiratory force.	Pressure.	Pressure change	Curves.
NaOH m/64	Unchanged or less.	Increased.	5 min.	Unchanged.	Unchanged.	25	26	30
m/32	Unchanged or less.	Much increased.	15 min.	Decreased or unchanged.	Decreased or unchanged.	24	29	31
m/8	Unchanged.	Increased.	10 min.	Increased.	Decreased.	24	27	32
m/4	Less or unchanged.	Increased.	10 min.	Unchanged or increased.	Decreased.	26	29	33

CURVE 30. Effect of m/64 NaOH injections.



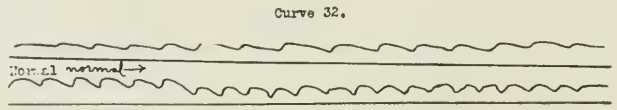
Upper, Hürthle curves of cardiac and blood-pressure changes; decrease in rate, increase in force and blood pressure for two minutes. Lower, gill-arch lever curves of respiratory changes unaltered.

CURVE 31. Effect of m/32 NaOH solutions.



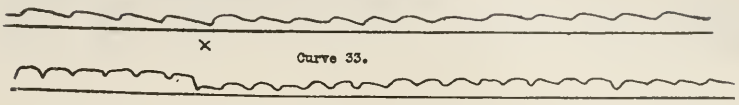
Upper, Hürthle curves of cardiac and blood-pressure changes show a first effect of two minutes of greatly increased force and slight decrease in rate of cardiac rhythm. The blood pressure increased for two minutes, respiratory rhythm decreased very little if at all.

CURVE 32. Effect of m/8 NaOH solutions.



Upper, Hürthle curves of cardiac and blood-pressure changes show increased blood pressure and rhythm. Lower, respiratory curves, increased rate but decreased force.

CURVE 33. Effect of m/4 NaOH solutions.



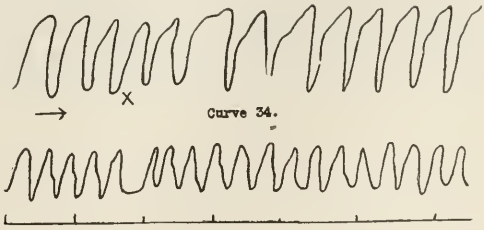
Upper curves, blood pressure and force of cardiac rhythm increased. Lower, respiratory activity decreased in force, rate increased.

From the series of experiments with different concentrations of urea solutions the conclusion is drawn that injection of urea solutions of high concentrations, 2m to 4m, increases force of respiratory and cardiac activity mainly. The rate is practically unchanged, and weaker solutions are quite indifferent on blood pressure, cardiac and respiratory activity. It has been found by Schröder[6] that selachian's blood normally contains 2.6 per cent of urea, and Baglioni[7] found that the selachian's heart beats longer in urea than in NaCl. According to Loeb it is due to the OH ions which are present when the dissociation of the urea occurs. A weak solution of m/20 of Na_2CO_3, to which a 2m urea solution has been added, greatly increased the force of cardiac action and blood pressure.

TABLE VIII. Effect of urea solutions.

Salt mol.	Heart rate.	Heart force.	Duration.	Respiratory rate.	Respiratory force.	Duration.	Pressure.	Pressure changes.	Curves.
Urea, m/50	Unchanged.	Unchanged.	15 min.	Unaltered.	Unchanged.	15 min.	20	20	
m/1	Unaltered.	Unaltered.	15 min.	Unaltered or less.	Unaltered or increase.	1 min.	21	21	34
2m.	Slight rise.	Slight increase.	2 min.	Unchanged.	Unaltered.	15 min.	20	20	35
4m.	Unchanged.	Increase.		Unchanged.	Increase.		22	21	36

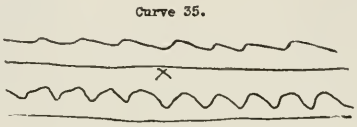
CURVE 34. Urea m/1.



6. Schröder. V. Zeitschrift für Physiologische Chemie, XIV, S. 596.
7. Baglioni. Zentralblatt für Physiologie, 1905, XXX, No. 12.

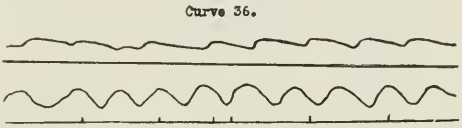
Upper, respiratory curve, with lever attached to gill arch, shows first decrease in rate for about one minute, then rate normal, force slightly increased. Lower, cardiac curve, with lever attached to apex. Cardiac activity unaltered.

CURVE 35. Urea 2m.



Upper, Hürthle cardiac record shows little increase in force and rate. Lower, respiratory rate and force unaltered.

CURVE 36. Urea 4m.



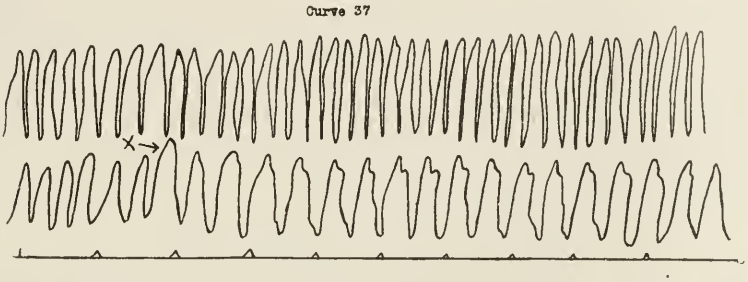
Upper, Hürthle cardiac curve; increased in force and pressure, rate unchanged. Lower, respiratory curve; force slight rise, rate unchanged.

The results obtained with standardized HCl solutions are tabulated in table IX. The weaker solutions, ranging from m/100 to m/64, increase for the first minute or two the force of the cardiac and respiratory and blood-pressure changes, and decrease or act indifferently on the rate of respiratory and cardiac activity. A stronger solution, m/32, for the first minute or two decreases the rate but usually increases the force of both the respiratory and heart action, and the blood pressure usually rises for the first minute; m/8 is toxic, but the respiratory rhythm continues several minutes after the heart ceases, or if it continues it is rapid and faint and the respiratory movements are continued with less force and rate. It is supposed that the stimulating action is due to the H ions. In all concentrations between m/100 and m/16 there is an initial increase in pressure and force, followed by a decrease in all activities before a return to either normal or less.

TABLE IX. Effect of HCl solutions.

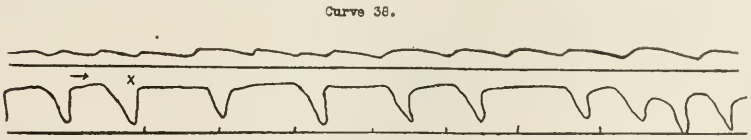
Salt mol.	Heart rate.	Heart force.	Duration.	Respiratory rate.	Respiratory force.	Duration.	Pressure.	Pressure changes.	Curves.
HCl m/64	Decreased.	Increased.	2 min.	Unchanged.	Increased or unchanged.	2 min.	19	20	37
m/32	Decreased.	Increased.	1 min.	Decreased.	Unchanged or increased.	1 min.	24	26	38
m/8	Rapid.	Weak.	1 min., then decreased.	Increased.	Unchanged or increased.	1 min., then decreased	21	10 0	39

CURVE 37. Effect of m/64 HCl on cardiac and respiratory activity and blood pressure.



Upper, gill-arch lever respiratory curve shows for two minutes increased force, rate unchanged. Lower, apex lever cardiac curve for two minutes increased force, decreased rate.

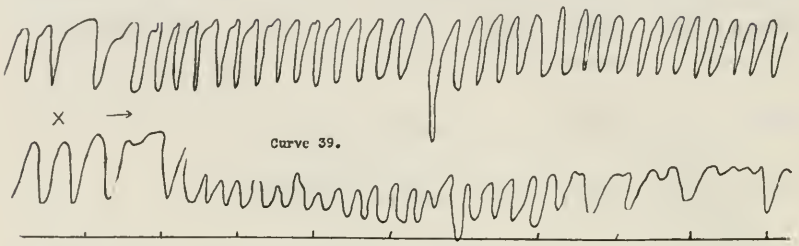
CURVE 38. m/32 HCl injection.



Upper, cardiac Hürthle manometer curve and blood pressure shows decreased rate and increased force and rise of blood pressure for one minute.

Lower, gill-arch lever record of respiratory activity shows rate less, force unchanged for one minute.

CURVE 39. Effect of m/8 HCl on cardiac, respiratory and blood pressure changes.



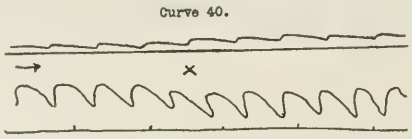
Upper, gill-arch lever respiratory curve shows increase at first of rate and force, then gradual decrease. Lower, apex lever curve shows at once fall in force and rapid heart-beat that soon becomes irregular and spasmodic before ceasing.

Injection of different strengths of NH_4Cl solutions show that weak solutions are quite indifferent. An m/8 solution increases blood pressure and force of respiratory movements, but an $m\frac{5}{8}$ depresses cardiac and blood pressure activities and greatly stimulates the expiratory phase of respiration, causing an irregular spasmodic rhythm for fifteen minutes, and this is replaced by a weak but regular activity.

TABLE X. Effect of NH_4Cl solutions.

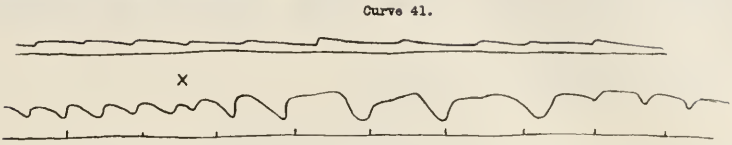
Salt. mol.	Heart rate.	Heart force.	Duration.	Respiratory rate.	Respiratory force.	Duration.	Pressure.	Pressure changes.	Curves.
NH_4Cl m 64	Unchanged or less.	Unchanged.	3 min.	Unchanged or increased.	Unchanged or less.	5 min.	26	26	
m 8	Unchanged or less.	Unchanged.	15 min.	Unchanged.	Expiration increased.	15 min.	26	28	40
$m\frac{5}{8}$	Much less.	Much less.	15	Long expiratory. irregular.	First increase, then regular or less.	15	26	22	41

CURVE 40. Influence of NH_4Cl m/8 on cardiac respiratory and blood-pressure changes.



Upper, Hürthle cardiac and blood-pressure curves show that rate and force are unchanged, blood pressure rose. Lower, respiratory curve; rate unchanged, force slight increase.

CURVE 41. Effect of m% NH_4Cl.



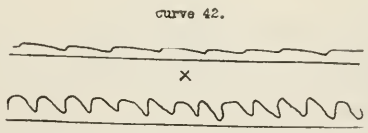
Upper, Hürthle cardiac and blood pressure show a decrease in cardiac activity and blood pressure. Lower, respiratory curve; for fifteen minutes prolonged expiratory phase and irregular rhythm, then weak but regular.

Effects of dehydrated chemically pure Na_2SO_4 solutions are most pronounced in the strong concentration of m/2 and m/1, both of which increase the force of cardiac, respiratory and blood-pressure activities, leaving the rate unchanged. The effect lasts longer with the weaker solution, and the after-effects are not, as with the saturated m/1 solution, a weakening of the rhythm and fall in pressure.

TABLE XI. Summary of Na_2SO_4 effects on respiratory cardiac, and blood-pressure changes.

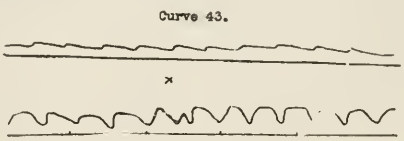
Salt mol.	Heart rate.	Heart force.	Duration.	Respiratory rate.	Respiratory force.	Duration.	Pressure.	Pressure change	Curves.
Na_2SO_4 m 64	Unchanged.	Unchanged.	15 min.	Unchanged.	Unchanged.	15 min.	26	26	42
m 2	Unchanged.	Slight increase.	15 min.	Unchanged.	Slight increase.	15 min.	26	27	43
m 1	Unchanged.	Slight increase.	5 min.	Unchanged.	Increased.	5 min.	27	29	44

CURVE 42. Effect of m/64 Na_2SO_4.



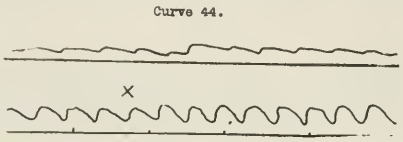
Upper, Hürthle cardiac and blood-pressure curve, and lower, respiratory, all show no change after injection of the solution.

CURVE 43. Effect of m/2 Na_2SO_4.



Upper, Hürthle cardiac and blood-pressure curves; rate unchanged, force and pressure slight increase. Lower, respiratory curve; rate unchanged, force increased.

CURVE 44. Effect of m/1 Na_2SO_4.



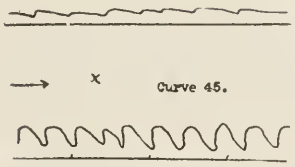
Upper, cardiac and blood-pressure curves, show slight increase in force and pressure, rate unchanged. Lower, respiratory; rate unchanged, force increased.

The effects of intravenous injections of $BaCl_2$ solutions are increased irritability and increased force and blood pressure, especially with weak solutions. Like most of the other salt solutions, it does not increase the rate of either heart or respiratory activity. In strong solutions it is toxic, producing at first irregular spasmodic cardiac and respiratory phases with strong diastolic and expiratory phases and with rise of blood pressure, or cessation of activity. The toxic effects can be avoided if small doses are injected with gradually increasing strengths, and the toxic effect is overcome by injections of $CaCl_2$ solutions.

TABLE XII. Effect of $BaCl_2$ on cardiac, respiratory and blood-pressure changes.

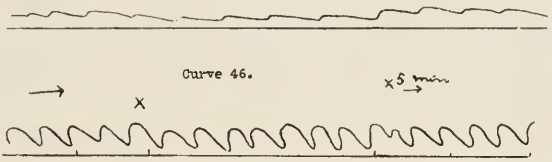
Salt mol.	Heart rate.	Heart force.	dura-tion.	Respir-atory rate.	Respir-atory force.	Dura-tion.	Pres-sure.	Pres-sure change	Curves.
$BaCl_2$ m 64	Un-changed.	In-creased diastole.	15 min.	Un-changed or slightly less.	Expira-tion in-creased.	2 min.	18 mm.	20 mm.	45
m 32	Un-changed.	Un-changed or in-creased.	1 min. 8 min.	Un-changed.	In-creased.	After 8 min.	16	16 18 14	46
m/8	Un-changed or slow or spas-modic.	In-creased irrita-bility.	2-5 min.	Stops or rapid spas-modic.		10-20 min. 2 min.	23	25	47
m/4	Toxic.			Toxic.					

CURVE 45. Effect of m/64 $BaCl_2$.



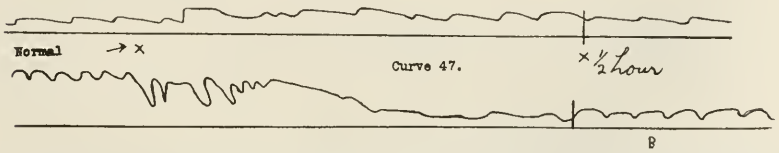
Upper, cardiac curve; rate unchanged, force and blood pressure slight increase. Lower, respiratory curve; rate unchanged, force increased.

CURVE 46. Effect of m/32 $BaCl_2$.



Upper, Hürthle cardiac curves; after one minute, rate, force and pressure unchanged. In five minutes, force and pressure increased. Lower, respiratory curve, shows rate unchanged, force increased.

CURVE 47. Effect of m/8 $BaCl_2$.



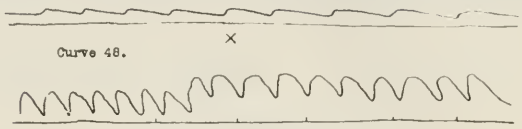
B half an hour after A. Upper curves of A and B, cardiac and blood-pressure records, show first spasmodic activity, then strong force and increased pressure. These activities decrease in half an hour but the rate continues unchanged. Lower, respiratory curve, shows first spasmodic action, then this stops for twenty minutes. In half an hour it is weak and slower.

The effect of distilled water passes off quite rapidly. For the first two minutes the rate of cardiac and respiratory activity is lessened and the force of the heart-beat and blood pressure slightly increased. The blood is rapidly affected and clots easily; soon the equilibrium of salts is again established and the normal action resumed.

TABLE XIII. Showing the effect of distilled water.

Distilled H_2O.	Heart rate.	Heart force.	Duration.	Respiratory rate.	Respiratory force.	Duration.	Pressure.	Pressure changes.	Curves.
3-4 cc.	Decrease.	Slight increase.	2 min.	Decreased.	Unchanged.	2 min.	24	26 24	48

CURVE 48. Effect of distilled water.



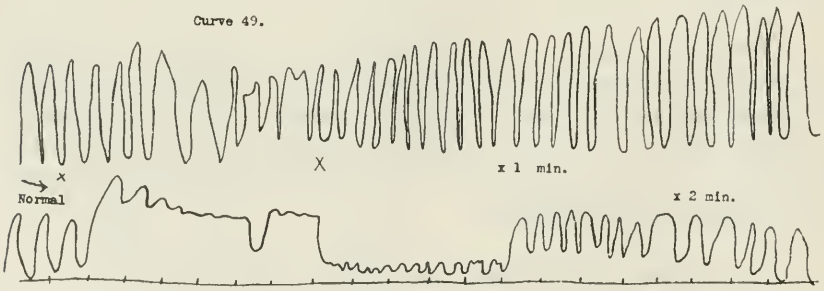
Upper, Hürthle cardiac and blood-pressure curves, show decrease in rate, slight rise in force and blood pressure for two minutes, then normal. Lower, respiratory lever, gill-arch curve, shows decrease in rate, force unchanged for two minutes.

Acid sodium phosphate solutions cause an increase in force of respiratory and cardiac activity, and for the weaker solutions at first also an increase in rate. Diastolic and inspiratory phases are often prolonged and the toxic effect is overcome by an alkali solution of sodium phosphate or one of $CaCl_2$.

TABLE XIV. Showing mean results of NaH_2PO_4 solutions.

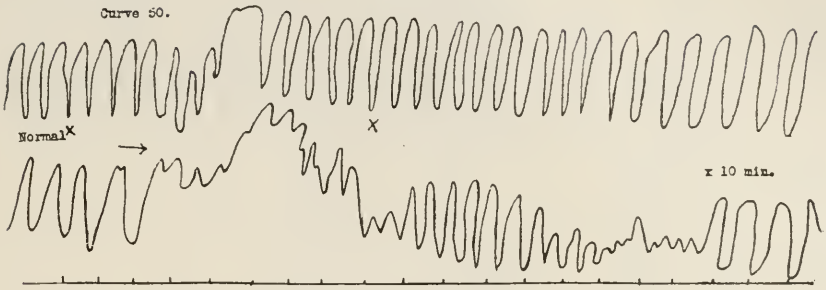
Mol. solution.	Heart rate.	Heart force.	Duration.	Respiratory rate.	Respiratory force.	Duration.	Pressure.	Pressure change	Curves.
m 64	Rapid to normal in two minutes.	Weak, increase.	1 min. 2 min.	Increased. Normal.	Less increase.	1 min. 2 min.			49
m 16	Increase.	Increase. Decrease. Normal.	1 min. 2d min. 10 min.	Unchanged.	Increased.	10 min.			50
m 8	Decreased. Normal.	Increased. Normal.	1 min. 5 min.	Increased.	Increased.	10 min.			51

CURVE 49. Effect of m/64 NaH_2PO_4 solutions.



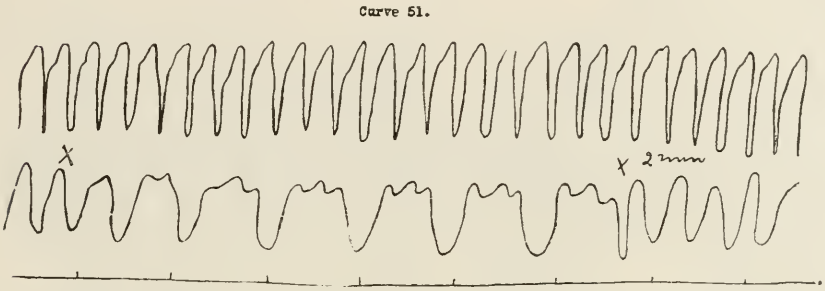
Upper records of respiratory activity before, during and following for two minutes the injection of an m/64 acid phosphate solution. First minute rate greatly increased, force less; within two minutes force gradually increased to slightly above normal and rate normal. The lower cardiac record shows first rapid contractions that increase during the second minute in force, becoming normal in rate and force in two minutes.

CURVE 50. Effect of m/16 NaH_2PO_4 solutions.



Upper, gill-arch lever records of respiratory activity, show increase in force, rate unchanged. Lower, cardiac lever, records first an increase in rate and force; second, rapid, shallow; in ten minutes quite normal in rate and force.

CURVE 51. m/8 NaH_2Po_4 solutions.



Upper, gill-arch lever records of respiration show increase in rate, and after two minutes also in force; inspiration prolonged. Lower, cardiac apex records. First minute prolonged diastole and increased force, followed by slower rate; in five minutes quite normal in rate and force.

TABLE XV. A general survey of the stimulating and depressing effects.

Stimulating salt mol.	Heart force.	Heart rate.	Respiratory rate.	Respiratory force.	Blood pressure.	Duration.	Depressing salt mol.	Heart rate.	Heart force.	Respiratory rate.	Respiratory force.	Blood pressure.	Remarks.
NaCl m 1 m⅝	Increased.	Unchanged.	Unaltered.	Increased.	Rose.	m⅝ 5 min. m 1 15 min.	NaCl m 1	Less.		Less.	Unchanged.		
NaCl m 2	Rise.	Systole long.		Inspiration long.	Rose.	2 min.	NaCl m 2	Less.	After 2 min. less.	Less.	Less.	Fall after 2 min.	Weak sol. stimulates, Strong depressess.
KCl m 32 m 8			m 8 Rose.				KCl m/32 m 8	Less.	Unchanged.	Less.	Unchanged or less.	Unchanged or less.	m⅝ toxic. Depresses.
$CaCl_2$ m 32 m⅝	Rose.			Rose.	Rose.	1-3 min.	$CaCl_2$ m 32 ⅝	Unchanged or less.		Unchanged or less.			m⅝ depresses. Often toxic.
$MgSO_4$ m 24 m 1					Rose.	1-15 min.	$MgSO_4$ m 64 m 1	Less.		Less.	Less.		Depressing.
Na_2CO_3 m 32 m⅝	Rose.			m⅝ Rose.	Rose.	1-15 min.	Na_2CO_3 m 32 ⅝	Less.		Unchanged.	Unchanged.		Strong cardiac stim. and raises blood pres.
Na_2HPO m 64 m 4	m 8 Rise.						Na_2HPO_4 m 64 m 4		m 4 less.	Unchanged.	Less.	Fall.	Weak sol. stimulates, strong depresses heart force.
NaOH m 64 m 4	Rise.		m 8+m 4 Rise.		Rise.	5-15 min.	NaOH m 64 m 4	m 64 m 32 Less.			Less.		Strong sol. decreases force of respir.
Urea m 1 4m	Rise.			Rise.			Urea m 1 4m	Unchanged.		Unchanged.	Unchanged.		Strong sol. stim. force. Otherwise indifferent.
HCl m 64 m 32	Rise.			Rise.	Rise.	1 min.	HCl m 64 m 32	Less.		Less.			Weak stim. briefly. strong sol. depres.
NH_4Cl m/64 m8				m/8 Rise.	m/8 Rise.		NH_4Cl m 64 m8	Less. m⅝	Less m⅝			m⅝ less.	m⅝ depress., m/8 stim. expir. and blood press.
Na_2SO_4 m 2 m 1	Rise.			Rise.	Rise.		Na_2SO_4 m/2 m 1						Stim. force and press.
$BaCl_2$ m 64 m/4	Rise.			Rise.	Rise.		$BaCl_2$ m/64 m 4						m/4 toxic, weak sol. stim. force. Pres. prolonged diastole.
Distilled water.	Brief rise.				Brief rise.		Distilled water.	Less.		Less.			Brief stim. for blood press. and cardiac force.
NaH_2PO_4 m/64 m/8	Rise.	Rise.	Rise.	Rise.			NaH_2PO_4 m/64 m/8						Weak sol. stim. rate and force, prolong inspir. & diastole.

TABLE XVI. Toxic and Antitoxic Solutions.

Toxic.	Antitoxic.	Curves.
2m NaCl.	$CaCl_2$ m 32	3
m⅝ KCl.	m⅝ NaCl	11
m⅝ KCl.	$CaCl_2$ m 32	12
m⅝ KCl.	$CaCl_2$ m 4	13
m 1 $NMgSO_4$	$CaCl_2$ m 8	14
NaH_2PO_4 m 4	Na_2HPO_4, or $CaCl_2$ m 16	
m 1 Na_2SO_4	$CaCl_2$ m 16	
$BaCl_2$ m 4	$CaCl_2$ m 8	
$BaCl_2$ m 4	NaOH m 8	
NaOH m 16	HCl m 100	

The following is a *résumé* of the conclusions drawn from the different experiments:

M⅝ NaCl increases the force of cardiac and respiratory rhythm and blood pressure, but is indifferent to the rate during the first five minutes. Weaker solutions are neutral, and a stronger, m/1, solution is rather depressing except to heart force and blood pressure, while 2m is generally depressing, prolonging systolic and inspiratory phases.

The different strengths of KCl solutions proved depressing to the activities under consideration. Diastole and inspiratory changes are prolonged and the toxic effect of an m⅝ solution is counteracted by CaCl m/32 or NaCl m⅝.

$CaCl_2$ solutions are indifferent or depressing to the rate of both cardiac and respiratory activities, but stimulating to the force and slightly so to the blood pressure. M⅝ solutions prolong systolic and inspiratory phases.

Solutions of $MgSO_4$ are depressing to the respiratory mechanism and cardiac rate, but at first stimulate heart force and blood pressure. Diastole and expiratory phases are prolonged and the toxic effects are neutralized by m/8 $CaCl_2$ solutions.

Na_2CO_3 solutions stimulate heart force and blood pressure and are indifferent to the heart rate and the respiratory mechanism. Their stimulating effect upon the force of cardiac activity is enhanced when the solution is combined with urea, and like the latter exerts a similar influence upon respiration and heart action.

Na_2HPO_4 solutions stimulate as a rule only the force of heart action. The blood pressure, heart rate, as well as respiratory activities, are generally decreased or unaltered.

Solutions of NaOH proved more stimulating to cardiac force and blood pressure than any of the other solutions that were employed. They were depressing to cardiac rate and respiratory activity, except in strong solutions they increased the rate of respiration. They affect the center that controls the force of the heart-beat oppositely from what they do the center which governs the respiratory force. Like other alkaline solutions, they may exert their influence by favoring oxidation.

Urea solutions, except the strongest, are quite indifferent to the functions under consideration. A 4m solution increases the force of both the cardiac and respiratory activities; possibly through the OH ions that are set free when dissociation occurs.

Weak HCl solutions produce initial stimulations for a brief period in cardiac and respiratory force and blood pressure, but depress the rate, and a stronger, m/8, solution is toxic for cardiac but less so for respiratory activity.

Weak solutions of NH_4Cl are indifferent. An m/8 has a slight augmenting effect on blood pressure and the expiratory phase, while an m/8 solution depresses blood pressure and cardiac rhythm, but heightens the force of the respiratory mechanism for a short time.

Following the injection of strong Na_2SO_4 solutions the force of respiration and heart action and height of blood pressure is increased, while the rate is unchanged. The addition of a weak solution of $CaCl_2$ is favorable.

The effect of a weak solution of $BaCl_2$ is increased force of cardiac and respiratory rhythm and a rise of blood pressure. Diastolic and expiratory phases are prolonged. The solutions are more toxic than other salts of the same concentration, and the toxicity is overcome by $CaCl_2$.

Injections of distilled water produce transient stimulating effects in the force of cardiac contractions and blood pressure, and depress the rate.

Weak solutions of NaH_2PO_4 accelerate the rate and force of heart and respiratory action. Diastole and inspiration are prolonged and toxic solutions are neutralized by Na_2HPO_4.

A consideration of the results tabulated in the foregoing

pages discloses the fact that increased force of cardiac activity is usually accompanied by increased force of respiratory action and blood pressure. But NH_4CL m/8, urea, and Na_2HPO_4 are exceptions. NH_4Cl increases blood pressure without increasing cardiac force. Urea produced increased force of respiratory and cardiac activity without raising blood pressure, and Na_2HPO_4 m/8 increases force of cardiac but decreases force of respiratory action. Moreover, most of the salt solutions of a definite concentration that augmented the force of cardiac also increased the force of the respiratory rhythm and proved either indifferent or depressing in their influence upon the rate of both of these activities.

The exceptions are $MgSO_4$ m/8, which stimulates force of cardiac but not that of respiratory activities and is depressing to rate, and NaOH m/8, that stimulates cardiac force and rate but not the respiratory rhythm.

The toxic effect of many solutions at certain concentrations was counteracted by definite strengths of other salts. Of these antagonistic solutions, $CaCl_2$ m/32 or m/8 proved most extensively favorable. It was interesting to learn that certain concentrations of some salt solutions prolong the cardiac systole and the inspiratory phases, while other solutions favor diastolic and expiratory phases. M/2 NaCl and also m⅝ $CaCl_2$ prolong systole and inspiration, while KCl m/8, NaH_2PO_4 m/8 prolong inspiratory activity and diastole. Moreover, strong solutions of $MgSO_4$, NH_4Cl and $BaCl_2$ prolong diastole and expiratory activity.

The salts that were especially depressing upon the cardiac and respiratory phases were KCl and $MgSO_4$. There are certain optimum per cents of salts and acid solutions, below or weaker than which the effect is stimulating or initiates temporarily increased activity, and above or greater concentration than which the solution inhibits or decreases activity or proves toxic. Moreover, increased blood pressure, as a rule, is accompanied by a decrease in rate of cardiac and respiratory activity.

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CONTENTS:

THE NUTRITION OF THE EMBRYO SAC AND EMBRYO IN CERTAIN LABIATÆ, ... *F. H. Billings.*

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THE NUTRITION OF THE EMBRYO SAC AND EMBRYO IN CERTAIN LABIATÆ.

BY F. H. BILLINGS.

Plates XI to XIV.

SOON after the publication of a paper on seed development, in which various sympetalous families were considered, the writer began an investigation of embryo-sac nutrition as found in the Labiatæ. Literature upon the subject indicated the presence of certain nutritive structures that resembled some of those described in the paper mentioned above. The structures consisted of outgrowths or specialized portions of the embryo sac which by enlargement frequently replaced considerable portions of the integument. The position and shape of the structures are characteristic in some instances of the family in which they occur. It is therefore one of the problems of the present investigation to ascertain what degree of uniformity prevails among a number of genera of the Labiatæ, and thus determine, if possible, whether any special type of embryonic structure is liable to become characteristic of the family. Though the number of species studied is but a small representation of the total number distributed over the earth, still, as will presently be shown, a great enough similarity exists among them to warrant the supposition that a like resemblance probably exists among the remainder. It would not be safe to extend such a conclusion to any family taken at random, inasmuch as some families are aggregates of groups, such as subfamilies, which may not be closely allied phylogenetically but which are associated on account of fulfilling certain taxonomic requirements.

One of the services that may ultimately be performed for taxonomy is that of testing the homogeneity of families. The results could be reached satisfactorily only after all the species of any given family had been examined as to their ontogeny. Taxonomically speaking, the Labiatæ are regarded as a fairly homogeneous family with well-marked characteristics.

Species whose common ancestors are not remote should show similarity in embryonic particulars, since these are doubtless the ones least influenced by environment.

No attempt was made to work out the stages preceding fertilization in every instance. Several species were examined, however, and the series of events constituting the earlier history of embryo-sac development were found to be identical.

The ovular primordium gives rise to a single megaspore mother cell, from which originates an axial row of four potential megaspores. The most deeply seated of the four develops into the ordinary type of an eight-celled embryo sac.

The growth of the embryo was followed in detail in *Lamium amplexicaule*, and it was found that the various stages in development correspond closely to the plan observed in most dicotyledonous embryos. However, it is not with the development of the embryo but with the behavior of the embryo sac that this paper has most to do.

Many of the writings of early investigators who worked along embryological lines show that there was little thought of assigning physiological significance to peculiar shapes assumed by the embryo sac. More recently quite a number of observers have entered the field, and they have shown the wisdom of correlating morphology and physiology. Bibliographies of their papers have been published from time to time, so that only the literature cited in the text, or very recent papers, will be given here.

The single and unusually thick integument of many Sympetalæ, including the Labiatæ, appear to serve a double function. The outermost layers become transformed into a seed coat, while the inner or remainder, wholly or in part, may become a nutritive tissue (Nährgewebe) which invites, as it seems, the digestive and absorptive activity of the endosperm. Sometimes the nutritive tissue is more or less localized, as can be seen from the deposits of starch in certain regions. In other instances the deposition of food material is general throughout

the integument, so that no special part would be likely to become a particular point of attack by the endosperm.

When the absorptive activity of the endosperm is largely centered in some outgrowth or differentiated portion of the embryo sac, the term "haustorium" is applied to such a portion. In instances where haustoria are not developed, the digestive and absorptive power is more or less equally distributed over the entire surface of the embryo sac. Where absorption is going on most rapidly, the cells directly concerned in the appropriation of the nutritive material are usually abundantly supplied with plasmatic contents. In case of the presence of a haustorium the endosperm cells lying adjacent to the base of the haustorium show the greatest richness in plasmatic contents.

The following genera and species of Labiatæ form the bases of the detailed description:

Lamium amplexicaule.
Stachys palustris.
Physostegia virginiana.
Leonurus cardiaca.
Brunella vulgaris.
Teucrium canadense.
Pycnanthemum lanceolatum.
Lycopus rubellus.
Mentha canadensis.
Salvia lanceolata.
Salvia azurea.
Monarda fistulosa.
Nepeta cataria.
Dracocephalum sp.
Scutellaria parvula.

Lamium amplexicaule.

This species will be given more detailed consideration than the others, for it will serve in a measure as a type of the family and also as a basis of comparison for the other species. The embryo sac, at the time fertilization is accomplished, contains the usual form of egg apparatus (fig. 1). The endosperm nucleus is large, spherical in form, and contains a vesicular nucleolus. The nucleus does not lie near the egg apparatus, as is the case in so many plants, but at the opposite end of the sac near the disintegrating antipodals. The contour of the sac shows a constriction which may be used to distinguish a larger upper, or micropylar portion, in which the egg apparatus lies, from a smaller, lower, or antipodal portion, in which the endosperm nucleus lies. The endosperm nucleus does not leave the antipodal region, but immediately after fertilization develops a tissue in its end of the sac. Double fertilization probably occurs, though it was not observed.

The egg responds to fertilization by elongating greatly, and pushing down into the forming endosperm tissue (figs. 2, 3). The elongation is at first due to the growth of the entire egg cell. A transverse wall soon separates the suspensor from the proembryo. It is thus seen that the cell which is to develop into the embryo is removed altogether from the micropylar portion of the sac. For a time this portion contains no active nuclei, the synergids being in a process of disintegration. But endosperm nuclei soon migrate into it through the space lying between the suspensor and the wall of the embryo sac. The nuclei are but few in number and they do not form tissue (fig. 4). From this time on, the two extremities of the embryo sac are very sharply distinguished. The antipodal end is soon filled with a compact growing tissue that surrounds the embryo. Increase in size of the tissue takes place rapidly, so that the micropylar portion shortly becomes the smaller (fig. 4). A remnant of nucellus can usually be seen as a disorganized mass of cells lying at one side of the micropylar expansion of the sac. For a considerable length of time the endosperm tissue extends only to the constriction, beyond which lies the micropylar region with its wandering endosperm nuclei. An examination of the integument cells surrounding this region shows that dissolution is in progress—due, of course, to the predatory activity of this part of the sac. The antipodal portion, with its endosperm tissue, exerts a similar absorptive influence, but the material absorbed by the latter is retained or used up in building more tissue, while that absorbed by the former is not, but is transferred to the endosperm tissue. The micropylar portion of the embryo sac may therefore be regarded as a haustorium. Evidence of the results of haustorial activity is seen in the unusual richness of plasmatic contents in the endosperm cells bordering on the haustorium. The presence of starch in the basal portion points to the same conclusion.

The nuclei of the haustorium do not form tissue, as has already been stated. In *Lamium amplexicaule* they take no definite position. Although they have the same origin as the nuclei of the endosperm tissue they differ considerably from them. The chief difference lies in their much greater size. These may attain a length of over thirty micromillimeters, which is greater than the average diameter of an endosperm

cell (fig. 5). The haustorial nuclei vary usually from twenty to thirty micromillimeters in diameter, but the smallest are much larger than any formed in the endosperm tissue, since these average only about five micromillimeters in diameter. Another difference is the much greater size of the nucleoli of the haustorial nuclei. In addition, the nucleoli are not vesicular, as are most of those in the endosperm tissue, but are solid. The large size of the nucleoli would seem to indicate an increased nutritive function on the part of the nucleus, especially in light of the theory that nucleoli represent reserve food substance. There is no evidence that the haustorial nuclei undergo division, either in *Lamium* or in the cœnocytic haustoria of any other of the Labiatæ investigated. There is some variance in the explanations of the peculiarity of these nuclei, but discussion of them will be reserved till the close of the paper.

The suspensor elongates during the growth of the embryo sac and finally attains an unusual length (fig. 6). Its course is for some time plainly visible in the haustorium and for a longer time in endosperm tissue. The portion nearest the embryo persists while the remainder slowly disintegrates. The appearance of the suspensor is such that at no time does it seem to serve as a conductor of food substances to the embryo, at least from any locality other than that of the endosperm tissue immediately surrounding it. It appears to have fulfilled its function when it carried the embryo from the haustorium down into the midst of developing endosperm tissue.

While the micropylar haustorium is transferring materials to one end of the endosperm tissue the opposite end is nourished by substances conducted through a vascular bundle that passes down the integument and terminates near the chalaza. The little depression or pocket in which the antipodals undergo disintegration is deepened until it forms a short canal, which extends from the endosperm toward the terminus of the vascular bundle. It does not merit the name of haustorium to the extent that the micropylar expansion of the sac does, since it exerts little or no absorptive influence upon the integument cells bordering it, but rather seems designed to facilitate conduction from the bundle. Its increase in length is not accompanied by a pronounced increase in diameter nor does it contain nuclei.

Later stages in embryo development show increase of the

endosperm tissue and a consequent encroachment upon the haustoria. Just when the micropylar haustorium ceases to function is hard to say. Its activity probably does not cease as soon as it begins to be encroached upon by the endosperm tissue. The nuclei in fact remain till late stages in seed development.

Stachys palutris.

The embryo sac seen in figure 7 presents markedly differentiated portions. The stage shown here is reached in the same manner as a corresponding one in *Lamium*. While the endosperm is beginning its formation in the antipodal end of the sac a number of nuclei migrate into the haustorium. They distribute themselves over the micropylar end of the haustorium, where the cytoplasm is chiefly located. The opposite end is distinctly vacuolated. It will be noticed that the constriction is very narrow. Through it passes the suspensor with an enveloping layer of cytoplasm. The regions adjacent on each side of the constriction are stored with starch, the result evidently of the absorptive activity of the haustorium. As in *Lamium*, the cells of the endosperm tissue nearest the haustorium are richer in plasmatic contents than those at a distance.

The canal that conducts from the terminus of the vascular bundle is comparatively long in *Stachys*. It is sharply bent about midway in its course, one arm running longitudinally to connect with the end of the vascular bundle.

Stachys and *Lamium* vary in the structure of their embryo sacs only in minor details, the main difference being the more definitely placed haustorial nuclei in *Stachys*. The embryo is nourished in both by the endosperm tissue surrounding it, this in turn being assisted in its growth by the activity of the haustorium. It is probable that the suspensor does not function in the conduction of materials to the embryo, on account of the disorganized condition of its cells. The food materials gathered by the haustorium are transmitted to the endosperm tissue through that part of the constriction lying around the suspensor.

Physostegia virginica.

This species has a peculiar appearing embryo sac when the stage shown in figure 8 is reached. Such difference as may be noted, when it is compared with *Lamium* and *Stachys*, is due principally to the direction of growth taken by the endosperm

tissue. If the growth had been uniform in all directions the long axes of the haustorium and endosperm tissue would have been approximately parallel. In *Phrysostegia* the endosperm grows in a one-sided fashion, producing a bend in the embryo sac of about ninety degrees. The haustorium is a club-shaped sac containing a few large nuclei. Its upper or micropylar end is vacuolated, while its lower end, adjoining the endosperm tissue, is densely protoplasmic. The suspensor is exceedingly long.

The position of the antipodal canal is peculiar in this species. It is located near the haustorium—a situation explained by the short length of the vascular bundle, as well as the one-sided growth of the endosperm tissue. The constriction existing between the haustorium and endosperm tissue is comparatively wide, with the result that the cytoplasm of the haustorium comes in contact with the endosperm tissue to a greater extent than in any other species examined.

Leonurus cardiaca.

Leonurus has a large haustorium with a contour much like that of *Stachys* (fig. 9). The haustorial nuclei have a more or less fixed position in that portion lying nearest the endosperm tissue. This is the reverse of the condition in *Stachys*, where the nuclei lie in the micropylar region. Their number varies from four to six. The definite position of the haustorial nuclei would suggest the presence of cell walls, but there was no evidence of them.

Leonurus bears a close resemblance to *Phrysostegia* in the proximity of the antipodal canal to the haustorium. The canal does not appear in the section shown in figure 9, so its position is indicated by the dotted lines. The lower portion of the endosperm tissue and its connection with the vascular bundle through the canal is shown in figure 10.

Brunella vulgaris.

This species possesses a large cœnocytic haustorium containing nuclei without definite position. In this respect it is like *Lamium*. The antipodal haustorial canal becomes laterally placed, but, unlike the two previously described genera, it remains near the base of the endosperm tissue.

The five genera thus far mentioned belong to the tribe Stachydeæ. No marked variations occur; in fact, they are

much more nearly alike than they are different. *Phrysostegia* appears to be the most divergent, but such divergence is really trivial. All are characterized by a large micropylar haustorium—a feature, however, which it shares with representatives of other tribes.

Teucrium canadense.

A glance at the diagram shown in figure 11 will show the relative position and size of the different portions of the embryo sac. The most noticeable difference between this species and those previously described is the relatively small size of the haustorium. The failure of the haustorium to enlarge much is doubtless mainly due to its proxity to the end of the beak-like extremity of the integument. There is but little room for enlargement. The haustorium contains a few nuclei that do not form a tissue. Whether this organ is really functional or not is difficult to determine with certainty. At most its activity can be only very slight, otherwise the extremity of the integument would undergo dissolution. The endosperm nuclei which are found in it do not have the size nor the altered appearance seen so frequently in vigorously acting haustoria. It would appear from this that alteration in the haustorial nuclei is to some extent at least proportional to the activity of the organ to which they belong.

Pycnanthemum lanceolatum.

The general configuration of the embryo sac is much like that of *Lamium* (fig. 12). The cœnocytic haustorium attains a large size, with the result that most of the micropylar portion of the integument becomes absorbed. The constriction between haustorium and endosperm tissue is soon obliterated, so that the two lie contiguous over a considerable area. The suspensor is long, as in the previously mentioned species, but owing to the size of the haustorium most of its length is found within the limits of this structure.

Lycopus rubellus.

Lycopus rubellus when contrasted with *Pycnanthemum*, which belongs to the same tribe, differs in two respects; the haustorium is small, and the constriction lying between it and the endosperm tissue is relatively long (fig. 13). The basal portion of the endosperm tissue extends in a beak-like process to the end of the vascular bundle. This process occupies the

position of the antipodal canal of previously described species. Its origin may be explained by a growth of the tissue into the canal, which it thus displaces. The haustorium contains but one or two nuclei with no formation of tissue.

Mentha canadensis.

The integument in this species is not extensive, yet there is a large cœnocytic haustorium present which closely resembles that of *Pycnanthemum*. Like *Pycnanthemum*, there is in *Mentha* an early obliteration of the canal connecting haustorium and endosperm tissue. *Lycopus*, on the other hand, represents the other extreme, in which the canal persists for a long time. *Pycnanthemum*, *Lycopus* and *Mentha* belong to the tribe Satureineæ.

Salvia azurea and *Salvia lanceolata.*

These two species will be considered together, as they present many points in common. As compared with the representatives of other genera, however, they show marked differences. In the first place, they are unique in having two haustorial outgrowths, one cœnocytic and one composed of ordinary endosperm tissue. In addition, there is a well-developed antipodal canal.

In order to follow better the development of the haustoria, it will be advantageous to examine the definitive embryo sac and consider some of the phenomena immediately following fertilization. The definitive embryo sac of *Salvia lanceolata* is shown in figure 14. It is short, and in comparison with the extensive integument is relatively insignificant (fig. 15). The shortness is the more noticeable when the amount of space occupied by the egg apparatus is taken into consideration. The embryo sac is filled with a reticulated cytoplasm, which is distinguished from that of *Lamium amplexicaule* and other species examined by the absence of vacuoles. The antipodals lie in the depression which marks the beginning of the canal to the vascular bundle. The small size of the embryo sac necessitates the proximity of the endosperm nucleus to the egg apparatus.

Fertilization is followed by a very *slight* elongation of the egg cell—a marked variation from the condition found in the species of other genera examined. The explanation for this difference lies in the fact that none of the space occupied by the definitive embryo sac is to be included in haustorium formation,

since elongation of the egg and suspensor is always for the purpose of removing the embryo from the sphere of haustorial activity. In *Lamium* approximately half of the sac becomes haustorium, and it is in view of this fact that the embryo is transferred for development to the antipodal region. The elongation of the suspensor in the majority of Labiatæ examined appears to terminate its function, for disintegration follows. In *Salvia*, on the contrary, there is reason to believe that it plays an important part in embryo nutrition. The cells composing it are short and relatively rich in plasmatic contents.

The first division of the endosperm nucleus results in the formation of a cell at the extreme antipodal end of the embryo sac. The wall cutting off this cell lies approximately in a plane at right angles to the long axis of the embryo and suspensor. The separating walls of cells produced in succeeding divisions are at first parallel to the first wall. The embryo is soon surrounded by endosperm tissue (fig. 16). One endosperm cell takes a position near the end of the suspensor for the purpose of entering directly into the formation of a haustorium. The growth of the endosperm tissue surrounding the embryo is greatest in a direction toward the upper part of the integument and approximately parallel with the vascular bundle. As a result, an endosperm process, cylindrical in shape, projects into the region where lies the most extensive portion of integument tissue (fig. 17). The outgrowth is evidently designed to reach the nutritive tissue remote from the main mass of endosperm. Functionally, it is a haustorium, differing principally from tissue-containing haustoria of certain other families of plants in the greater number of cells. Figure 17 shows a young haustorium of *Salvia lanceolata*. In its maturer stages, seen diagrammatically in figure 19, it is composed of much elongated cells. Such differentiation suggests conduction as a function. The elongated cells lie principally in the axis of the haustorium with their long axes parallel to that of the haustorium. The peripheral cells serve as digestive and absorptive cells, while those of the interior of the haustorium are conductive. The products of its activity are transferred to the main mass of endosperm which it thus serves as an absorbing organ.

The other haustorium is cœnocytic, and its activities are directly concerned with embryo nutrition through the suspensor. It is not a structure developed from the suspensor, though

it continues it, in a way, out into the integument. It recalls some of the haustorial outgrowths in the suspensor cells in certain Orchidaceæ[2] and Rubiaceæ.[3] In *Salvia lanceolata* two endosperm nuclei take part in haustorium formation; more than two in *Salvia azurea* (fig. 18). In both species one end of the haustorium completes the basal or proximal portion of the suspensor. In *Salvia lanceolata* more of the suspensor is surrounded than in *Salvia azurea*. In the former the suspensor becomes bent while in the latter it remains straight.

The haustorium grows outward through the integument, taking a direction nearly at right angles to that taken by the other haustoria. The purpose of the cœnocytic haustorium is to dissolve the integument cells surrounding it, but it is unique in communicating the products of its activity to the suspensor. Attention has already been called to the striking differences between the *Salvia* suspensors and those of the other Labiatæ examined. As the former take part in embryo nutrition their cells present an appearance betokening activity. Instead of losing their protoplasmic contents or undergoing dissolution, as in instances where excessive elongation takes place, the suspensor cells of *Salvia* are healthy appearing, resembling the endosperm cells in this respect not a little.

The cœnocytic haustorium does not attain the size of the one composed of tissue (fig. 19). As in similar haustoria previously described, the nuclei are larger than those of the endosperm tissue.

A canal, bent at nearly right angles, is formed between the endosperm and the vascular bundle. There appears to be no nucleus in it, but granular material resembling cytoplasm is found along the side walls and at the end. As the main body of endosperm pushes outward at the expense of the integument cells, the canal does not suffer for a time (fig. 20). Instead, the endosperm becomes laid down around its proximal end. This gives the appearance of the canal piercing the tissue. The canal forms a direct communication with the vascular bundle, serving probably as a conduction to the endosperm.

Monarda fistulosa.

This species is patterned after *Lamium* rather than after *Salvia*. There is a large cœnocytic micropylar haustorium which does not differ materially from that of *Lamium*. A few nuclei are present, though of a relatively smaller size. The

embryo sac is narrow and the suspensor is very long. There is no antipodal canal, but the endosperm tissue bends toward the terminus of the vascular bundle in the form of a process.

Nepeta cataria.

The haustorium of *Nepeta cataria* is cœnocytic, and contains four nuclei that occupy a more or less definite position at its base or near the place where the suspensor passes into the constriction (fig. 21). The haustorium is relatively small, containing much less than half the length of the suspensor.

Dracocephalum sp.

This varies from the other species of Labiatæ examined in the character of the outline of the endosperm tissue. In the other species this tissue enlarges quite uniformly, presenting a smooth or entire outline when sectioned. The outgrowths in *Dracocephalum* have no definite position or form and hence are not to be regarded as other than integral portions of the endosperm tissue and not haustoria (fig. 22). The haustorium is much elongated, as is the endosperm tissue. The embryo lies in the upper portion of the latter, being attached at the end of a very long suspensor.

Scutellaria parvula.

The bent embryo sac of *Scutellaria,* resulting in a bent embryo in the ripe seed, is of course well known to taxonomists. It conforms to the other species in Labiatæ in possessing a haustorium, but located, as it is, at the extreme tip of the ovule, its growth is greatly limited, so that it remains small (fig. 23). The endosperm is elongated and tapers at the base into a hook-like process whose end lies near the terminus of the vascular bundle.

DISCUSSION AND CONCLUSIONS.

In a large number of plants, especially those in which two integuments are present, the embryo sac assumes a somewhat elliptical or oval form in longitudinal section, with an approximately entire outline. The nutrition designed for growth of the endosperm may be absorbed fairly uniformly over the entire surface of the sac, or it may be absorbed more rapidly at one point than at other points, but in either case the elliptical or oval outline is maintained. If added organs mean increased specialization, then embryo sacs of the type just mentioned,

without special absorptive structures, may be regarded as a simpler, less differentiated, perhaps more nearly primitive, sort.

In some instances the innermost cell layer of integument, which borders on the nucellus or else on the embryo sac, is specialized into a digestive layer, whose activity is directed against the remaining integument for the benefit of the embryo sac. The name "tapetum" has been frequently applied to this layer, but its use is justified only on account of the nutritive function it performs. Goebel[4] proposes the term "epithelium" as a substitute. Three characteristics usually pertain to the epithelium: first, it remains intact for a longer period than the integumental layers adjacent; second, its cells become differentiated in form or contents from those of the remaining integument; third, it apparently exerts a digestive action. The digestive action is doubted by some, among whom is Schmid,[5] who ascribes a protective function to it. Since the species of Labiatæ herein described do not develop an epithelium, it is without the province of this discussion to do more than call attention to the fact that Schmid challenges the results obtained by the "Goebelische Schule," thus showing that the problem is open for further investigation.

The Labiatæ, in common with some other sympetalous families, depart from the type described for many plants having two integuments by differentiating haustoria. The haustorium implies increased absorptive activity in one portion of the embryo sac, but not necessarily cessation of the function elsewhere. Among the labiates studied, all (with the single exception of *Salvia*) have a micropylar haustorium of some sort. In most of the species it is a well-developed structure, exhibiting manifest activity as a nutritive organ. But in such species as *Scutellaria parvula*, *Teucrium canadense*, and *Lycopus rubellus*, it is of small size, and its usefulness may with safety be said to be either greatly reduced or else obsolete. Whether such a condition really represents actual reduction from a previously more highly developed state, or whether it is primitive in its nature, is a problem yet to be solved. The much elongated suspensor is here offered as evidence favoring the former view, since the purpose of elongation is believed to be the removal of the embryo from the region of the haustorium. Extraordinary length in proportion to the size of the haustorium

might therefore mean that shortening of the former did not accompany reduction in size of the latter. Conditions external to the embryo sac may have had something to do with haustorium reduction in such a species as *Scutellaria parvula,* where narrowing of the integument to a beak left but little tissue to be exploited.

The nuclei in the cœnocytic haustorium merit interest on account of the extraordinary size and appearance some of them attain. Such nuclei are found in other families where similar haustoria exist. They have been described by Balicka-Iwanowska,[6] Schmid[5] and others. That they are transformed endosperm nuclei is of course easy to observe. Knowing the kind of work the haustorium is called upon to do, one might expect increase in size, both of entire nucleus and also of nucleolus, on account of extraordinary nutritive function. The loss of power to divide accompanies the development of this function. According to Schmid,[5] the nuclei should be considered degenerate structures, whose condition has been produced by excessive nourishment, as is attested by loss of power to divide. Instances of like nature are not limited to embryo sacs, but occur in mycorrhiza and in animals. There is room for difference of opinion, however, as to the governing principle underlying such nuclear change. It is at least open to investigation whether the increase in size is a direct result of degeneration, due to unusually favorable conditions regarding food supply, or whether it is due to the added functional responsibility demanded of them by the haustorium. It is questionable whether either failure to undergo division or exceptional abundance of nutriment should be used as a test of degeneracy. As evidence against the latter view, attention is called to the normal appearance of the nuclei in the cellular haustorium in *Salvia* and those in the endosperm cells adjacent to a cœnocytic haustorium. Both are in very favorable condition as to food supply, yet there is no nuclear enlargement. It would appear that cœnocytic structure is conducive to such enlargement, but it cannot be merely a question of food supply. A difference is to be noted in the lack of cell walls, which in a tissue may possibly exert a limiting influence on increase of size in nuclei. Another difference is seen in the relatively small number of nuclei in a cœnocytic haustorium. It might be difficult to prove, however, that for this reason the work demanded of each

nucleus would be greater, though of course there is a possibility that it might be true.

Haustoria have either indefinite or more or less definite positions of their nuclei. Walls might be expected in instances where the nuclei are definitely placed. Balicka-Iwanowska[6] found a very delicate gelatinous membrane present in certain instances of this sort. No walls were evident, however, in any of the micropylar haustoria of the Labiatæ.

Indefinite location of nuclei are associated with irregular form of haustorium, while those having a more nearly fixed position are found in such as have an approximately symmetrical form.

The Labiatæ investigated generally have long suspensors, which are associated with the presence of micropylar haustoria. An exception is seen in *Salvia*, which has a short suspensor and no micropylar haustorium. The direct results of suspensor elongation are the removal of the embryo from the haustorium and its transfer to the vicinity of the center of the growing endosperm tissue. These results are doubtless sufficient to serve as causes for suspensor elongation. It is at least evident that a position within the haustorium would not be as favorable as a position without in so far as the products of haustorial activity are concerned. The endosperm tissue itself exerts a digestive action on the integument, and it also receives the nutriment from the haustorium, hence this tissue is more favorable for embryo development than the haustorium alone. Although integument cells are destroyed by the haustorium, there is no reason for believing that those of the embryo would likewise be, since endosperm tissue bordering on the haustorium is in no way affected by its digestive action. There is, therefore, no reason for thinking that suspensor elongation is to remove the embryo from the predatory action of the haustorium.

In general, it does not appear that the suspensor functions as a conductor of nutrition to the embryo. Evidence for this view is found in the collapsed condition of the suspensor through nearly its entire length, especially in that part lying within the haustorium. The greater portion of it is apparently without cell contents of any sort, and may or may not be continuous from the micropylar end of the embryo sac to the embryo. It would be expected of a cell or tissue that is serving

actively as a means of translocation of food materials that some vestige of life would be discernible. In *Salvia*, for instance, a healthy, vigorous condition of the suspensor cells accompanies activity in food transmission. In all the species examined (except *Salvia*), the only suspensor cells that appeared to be living were those immediately adjacent to the embryo. The nutrition of the embryo is accomplished through absorption over its entire surface, whereas in *Salvia* an added source of nutriment probably lies in the conducting power of the suspensor.

The length of the suspensor is roughly proportionate to the size of the haustorium through which the embryo has to be transported. Usually the movement is past a cœnocytic structure to a tissue. An instance is to be noted, however, in *Myoporum*[1] (Myoporaceæ), in which the growth is directly through one portion of the endosperm to another. The beaked portion of the endosperm is apparently a remnant of what may once have been a cœnocytic haustorium, but in which the cœnocytic condition has been lost.

The integument varies in thickness and extent in the different species. Of course, it is in those in which it is most extensive that the largest haustoria are possible. Through the integument in each case there runs a vascular bundle which terminates near the antipodal region. A slight outpocketing of the embryo sac is found extending into the integument toward the end of the bundle. Later it may develop into a canal without nuclei, or into a process of the endosperm. Its function in all cases is evident—to facilitate the passage of nutriment from the vascular bundle to the endosperm.

In summing up the characteristics that are common to the species described in this paper, with the exception of *Salvia*, they have been found to possess three that in the future may be shown to belong to the family as a whole. They are the micropylar haustorium, the much-elongated suspensor, and the antipodal canal or process. Marked variations from a common type, such as are found in *Salvia*, suggest a taxonomic rearrangement, even though the usual macroscopic characteristics resemble those of the family in which the varying species is placed. In a previous paper,[1] for instance, attention was called to the striking difference in the ovular structure of the Menyantheæ when compared with the coördinate subfamily

Gentianeæ. The two have since been raised to family rank, probably for other reasons, yet it is interesting to note that the structure of the ovule justified the wisdom of the change. In this way can a study of sporangial, gametophytic and embryonic structures be of service in establishing more natural relationships and groupings.

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CONTENTS:

MITOSIS IN THE ROOT-TIP CELLS OF PODOPHYLLUM PELTATUM, *A. Richards.*

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MITOSIS IN THE ROOT-TIP CELLS OF *PODOPHYLLUM PELTATUM.*

BY A. RICHARDS.

Plates XV and XVI.

(Contribution from the Botanical Laboratory of the University of Kansas.)

THE work, the results of which are herein presented, was undertaken during the summer of 1907, under the direction of Prof. W. C. Stevens, whom I have to thank for his kindness and much helpful advice. My thanks are also due Mr. F. A. Hartman for helpful suggestions.

In discussing the root-tip cells of *Podophyllum peltatum*, I shall use the following outline:

I. Methods.
II. Resting cells.
  A. Nucleus.
    1. Nuclear membrane.
    2. Chromatin.
    3. Achromatin.
    4. Nucleolus.
  B. Cytosome.
    1. Cell wall.
    2. Cytoplasm.
    3. Archoplasm.
III. Dividing cells.
  A. Prophase.
    1. Nucleus.
    2. Cytosome.
  B. Later phases of division.
    1. Chromatin.
    2. Achromatin and cytoplasm.
IV. General considerations.
  A. Achromatic and archoplasmic structures.
  B. Individuality of chromosomes.

METHODS.

The root-tips of *Podophyllum peltatum* are peculiarly fitted for the study of mitosis in the vegetative cells of plants. The cells are larger than those of the onion root-tip, and in properly stained material the cell organs, especially the chromosomes, are to be seen with almost diagrammatic clearness.

The material used in this study was collected during the latter part of March and fixed in Flemming. For staining the sections three methods were used: Haidenhain's iron-hæmatoxylin (some sections counterstained with orange G), the safranin-gentian violet-orange G stain, and a combination of these two. Satisfactory results were obtained with slides stained in hæmatoxylin, both with and without the counterstain; the three-color method also gave fair results. Only a few sections were successful with the combination method, but they were promising; without doubt the method will repay careful experiment. It was followed as given by Schaffner (2).

THE RESTING CELL.

The most typical resting cells are not often to be found at the tip of the root, for this, of course, is the region of greatest mitotic activity and the resting stages are very short, but back from the tip as much as two millimeters. Farther from the tip the cells are apt to be plasmolyzed in fixing.

The nuclear membrane of the resting cell normally disappears as soon as the cell begins division; it is, however, quite constant in its appearance and staining reaction, and varies only slightly in thickness. It appears to stain very deeply with chromatin stains, a fact which is probably due to the peripheral arrangement of the chromatin granules, as seen in figure 1. These chromatin masses are arranged over the linin network of the nucleus in large or small patches, depending on the age of the cell, *i. e.*, nearness to the tip.

In examining the achromatic structures of the cells of *P. peltatum* I have had considerable difficulty, especially in the stages of mitosis. In some cells they can be seen quite clearly; in others, which appear to be equally well fixed and have been treated with exactly the same methods, they cannot be seen at all. Owing to this irregularity in their staining capacity, I have not been able to work out their history accurately.

The nucleoli of these cells are very interesting. They vary

in number from one to several—rarely more than four—and in size and shape. In general they are irregular-spherical, but may be compressed into different shapes. The variation in size, which is considerable, depends on the age of the cell. As the time for division approaches they grow smaller, finally disappearing about the same time as the nuclear membrane. This last fact sustains the conclusion that the nucleolus is simply a storehouse for food material for the rest of the cell.

In most cells up to the time of division there is noticeable a peculiar vacuolated condition of the nucleus, and in these vacuoles lie the nucleoli. Figure 1 shows two such cells, one of which has a single large nucleolus surrounded by a vacuole and the other three. The term "vacuole" for the clear space surrounding the nucleoli may be misleading. Experiments seem to show that this colorless space contains something more than a watery fluid, which is extracted by dehydration. By subjecting the roots of *Zea mays*, *Vicia faba*, and other plants to strong centrifugal force, Mottier (1) found that the nucleolus with its surrounding clear space was thrown out of the nucleus into the cytoplasm. "The nucleolus was still surrounded by the space, a fact that seems to show that the colorless substance has greater specific gravity than the other contents of the nucleus. The colorless substance may represent the unorganized nucleolar material."

The cell wall of the resting cells stains much like the nuclear membrane and is only slightly thicker.

The cytoplasm stains fairly dark with iron hæmatoxylin, and shows its fine reticular structure quite plainly. Scattered uniformly over the threads of the reticulum are large granules. The cytoplasm of the cell stains slightly denser than the nuclear sap.

With regard to archoplasmic structures, not the slightest evidence was seen to indicate that such structures as have been described by Schaffner are ever present: *i. e.*, centrosomes and centrospheres.

DIVIDING CELLS.

The plane of division in these cells is mostly at right angles to the axis of the root. This rule, however, is by no means invariable, for numerous cases have been found with the division planes parallel to, or at an angle of forty-five degrees with, the longitudinal axis (figs. 14, 20).

When the nucleus begins division the chromatin masses arrange themselves in a spireme (figs. 2, 3) and the linin reticulum can no longer be seen. Perhaps the network has drawn tighter, the threads stretching out to form a framework for the spireme. This stage has been called "close mother skein" (Schaffner). In figure 2 the nucleoli are still present, but they are now without the surrounding clear spaces.

The spireme soon becomes looped with the heads pointing toward the poles. I have not observed any connection between this fact and the fact that the chromosomes are J- and U-shaped. The segmentation of the spireme does not seem to occur regularly near the equator of the nucleus, as would be necessary to make the heads of the chromosome loops identical with those of the spireme loops.

At about this stage the nuclear membrane disappears, as do the nucleoli. There is, of course, variation about the time of disappearance, for the membrane is still present in figure 4, where the granules have split to form a double spireme. This split is very clearly shown in figures 5 and 6. The spireme granules here have segmented to form the chromosomes. Immediately after segmentation the chromosome granules condense and the segments shorten, thus giving the apparently solid character to the chromosomes. In figure 6 the two lower segments have lagged behind the others in condensation.

At this stage or earlier the *anlage* of the spindle should appear, for in the next stage observed the chromosomes were arranged on the bipolar spindle in the metaphase. The origin of the spindle was not observed, however, nor were any traces of a multipolar spindle seen. This may be due to any one of the three causes: the duration of the multipolar spindle may be short; the spindle substance at this stage may not take the stain readily; or the bipolar spindle may have been formed in the manner usual in the cases of higher plants, but with the omission of the multipolar stage. Of these three hypotheses for the absence of the multipolar stage, the third seems, perhaps, the best from the evidence in hand. The probability of the hypothesis decreases when we consider that the central spindle fibers stain more deeply than the traction fibers. No centrosome or centrosphere was seen in these cells, although in one or two cases a massing of protoplasmic granules at the poles of the cells might have been taken on a superficial examination for a centrosphere (figs. 7, 11). It was not difficult to de-

termine, however, that such was not the case, and it seems quite certain that the spindle is formed without the influence of other archoplasmic structures.

In most cells there is no metaphase for the entire chromosome mass, *i. e.*, an equatorial plate, in these cells, but each chromosome passes through the stage without waiting for the others. Figures 7 and 11 are the only approach to such a condition, and even here there is some lack of uniformity in the division of the chromosomes. Figures 8, 9 and 10 show the usual condition of the equatorial plate. Figure 10 shows the longitudinal split of the undivided chromosomes very clearly. This cell was crushed, but the crushing served to bring out the split all the better.

During the metaphase the first signs are seen of the concentration of the cytoplasm at the center of the cell, where the new wall is to be formed, and the consequent vacuolation of the cytoplasm at the poles. (This phenomenon is the usual occurrence in these cells but there are numerous instances where it is only slightly marked.) This concentration seems to aid in the construction of the new cell plate, for the more marked the concentration the more rapid the cell-plate formation.

In regard to the division of the chromosomes nothing unusual was observed. The chromosomes divide and pass to the poles as in most forms. In passing up to the poles the chromosomes usually turn with the short arm of the J toward the center of the spindle. One chromosome seemed to stand out from the rest slightly and was especially marked by its size; this was the long chromosome *m* (figs. 9, 14). Polar views of the anaphase present the best opportunities for counting the chromosomes, but there is much uncertainty even here, owing to the difficulty of getting all of the plate in one section or of tracing it through neighboring sections. Fourteen chromosomes were counted in about a dozen cells, but this, of course, is insufficient evidence on which to base a decision.

Arrived at the poles the chromosomes fuse end to end and then form a loose daughter "skein." This "skein" becomes a close one and the chromatin forms a dense mass at the poles. The remainder of the nuclear reconstruction consists in the formation of the membrane, the distribution of the chromatin granules in the nuclei, the appearance of the linin network and the formation of new nucleoli. It is a general rule that the nucleoli arise on the side of the cell nearest the new cell wall.

While the reconstruction of the nuclei has been in progress, several changes have occurred in the spindle and the cytoplasm. As soon as the concentration of the cytoplasm is complete the spindle broadens out somewhat. Figure 23 shows a maximum bulging, while figure 22 is perhaps a minimum. Figure 22 shows an unusual phenomenon in the process; the majority of the central spindle fibers (only the central fibers now remain) seem to have become free at their polar ends and to have shortened towards the center, staining very darkly in this region. The threads disappear as soon as the cell walls are formed. It is difficult to determine what the bulging out of the spindle and the concentration of the threads and cytoplasm signify, but it seems probable that the threads contain some substance useful in the construction of the new cell wall. This suggestion is in line with the work of Strasburger (4) and Haberlandt (5), who have discussed this phenomenon of the spindle in detail.

The rate at which these processes occur varies. One may find a nuclear membrane before the cell plate has started (fig. 20), or he may find the cell plate well started while the chromatin is still in the loose daughter "skein" (fig. 19).

GENERAL CONSIDERATIONS.

Achromatin and Archoplasm.—In regard to the origin of the spindle Schaffner concludes that, in root-tips of the onion and of *Sagittaria,* at least, the multipolar spindle is due either to pathological causes or to "improper manipulation in preparing the sections," and that a bipolar spindle is formed not by the transformation of a multipolar stage but under the influence of a centrosome and centrosphere as commonly described for animals. As previously stated, I find no evidence whatever for concluding that such archoplasmic structures are present.

Although no traces of a multipolar spindle have been seen here, it is not necessary to assume that a centrosome is present to guide the formation of the bipolar spindle, as the fibers themselves may possess sufficient directive energy to bring about the bipolar form.

Individuality.—A single bit of evidence was found in support of the theory of individuality of the chromosomes in vegetative cells. In several of the cells there is an unusually long chromosome, *m,* in general dividing before the others in the cell. Although this meager bit of evidence is by no means conclusive,

it points toward the view that while the cell is the unit of structure the chromosome is the unit of potentiality, and that the chromosomes themselves may all differ in structure and, if in structure, also in potentiality.

An interesting problem concerning these root-tip cells is the relation of the cells to the entire tissue and the cytological processes of later stages of embryonic growth. Material for this study is not at hand at this time, but I hope to be able to trace out these processes at some subsequent period.

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NOTE.

The drawings of the *Podophyllum* root-tips were all made with the aid of a camera lucida (B. & L.) A C. Reichert 1/12 objective was used and with it a B. & L. ½-inch ocular for the larger figures and a ¾-inch for the smaller, making a magnification of 2466 and 2000 diameters, respectively.

Figures 9, 13, 14, 15, 16, 18, 20, 22, 23, 24, were made from material stained with the Flemming three-color method. The others were made from sections stained with the iron-hæmatoxylin method.

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CONTENTS:

KOEBERLINIA SPINOSA ZUCC.: AN ECOLOGICAL STUDY OF THE ANATOMY OF THE STEM AND SOME OTHER PARTS, ... *Miriam Sheldon.*

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KOEBERLINIA SPINOSA ZUCC.:

AN ECOLOGICAL STUDY OF THE ANATOMY OF THE STEM AND SOME OTHER PARTS.

BY MIRIAM SHELDON.

Plates XVII to XXV.

INTRODUCTION.

SOME plant forms are peculiar and striking. Those of the desert are particularly individual, many being even grotesque in their chance variations. The choice of one of these plants for study was suggested by Professor Stevens, of the Botany Department of the University of Kansas. Accordingly, after sectioning and examining about fifty or sixty plants, I selected and studied three more carefully. Of these the subject of this sketch is perhaps the most interesting.

The material for this study was obtained in the summer of 1908. In July of that year collections of about sixty or seventy different species were made by Mr. L. M. Peace, of the University of Kansas laboratories. These were taken from the region around about Tucson, Ariz., representatives of some species being taken from several habitats, as from mesa, wash, irrigating ditch or hill top. As the short summer season of rains had just begun some of the plants were obtainable before the leaves had appeared. Specimens were, of course, also taken after the leaves came out. The jars with their preserving fluid (two per cent formalin) were taken into the field, and the plants put into these as soon as collected. In many instances the whole plant was secured, one jar containing the root, stem, leaves and flower or fruit of the same plant. It will be seen that this collection is particularly valuable because

of the great care taken in obtaining it. Many thanks are due Mr. Peace on this account, as well as for numerous verbal explanations and descriptions of the desert, the vegetation and the individual plants.

The literature dealing with the desert plants is, as is well known, somewhat meager. So far very little more than a description or a mere mention of *Koeberlinia* has been found. Gray describes it in his Plantæ Wrightianæ, and places it with the Rutaceæ. Engelmann mentions it twice in his works: once in his review of the Wislizenus plants and once as erroneously numbered by Emory among his Cactaceæ of the Southwest. Bentham and Hooker describe it under the family Simarubaceæ. The Ailanthus, or "Tree of Heaven," is perhaps the most familiar representative of this family with us northern dwellers among mesophytic forms. John Charles Van Dyke alludes to the "crucifixion thorn" in "The Desert." He says he has met with it in several localities although it is reported as "very scarce." Several travelers in Mexico and the Southwest have made collections of this plant or have reported it. Prof. Charles Bessey, of the University of Nebraska, in the "Burro Thorn" (*Holocantha emoryi*) finds a plant of great interest, if not one wholly as attractive morphologically, if one may judge by the brief account he was able to give for lack of the "oft promised material."

A description of the plant as a whole has not been found. We do not know that anyone has ever had the hardihood to dig up a root. It is said to make an impenetrable barrier, so that a plant three feet high is of such dense growth that the main stem is hardly to be seen. Among the earlier collectors of the plant might be mentioned Chas. Wright, Dr. Josiah Gregg, Gen. Wm. H. Emory and Dr. N. Wislizenus. The plant is sometimes called "Junco." It seems as the northern border of Mexico is approached the individual plants become more stunted and less numerous than farther south. The plant is thus described by Sargent:

"Leaves, not more than one inch long. Flowers, appearing in May and June, about one-fourth inch in diameter. A bushy tree, rarely twenty to twenty-five feet high, with a short, stout trunk sometimes six to eight feet long and a foot in diameter; more often a low-branching shrub forming impenetrable thickets, often of considerable extent. Wood very hard, heavy, close-grained, dark brown somewhat streaked with orange;

becomes almost black on exposure, with thin yellow or nearly white sapwood of twelve to fifteen layers of annual growth. Distribution: Dry gravelly mesas and foothills, valley of the Lower Rio Grande, Texas, westward to southern through northern Mexico."

The four or five plants seen by Mr. Peace were of various sizes, the largest—the one from which the specimens were taken—being about three feet wide and very compact in growth. The branches were pale green in color, no leaves, the flowers whitish to cream color. This was about three miles southwest of Tucson.

As far as observed every branch is a thorn, some of them a little blunt at the end and not tipped with the brownish needle-like point. The thorns vary from 1.5 cm. to 7 cm. in length, being from 1 mm. to 4 mm. in diameter at the base. The largest stem obtainable for study was about 4.5 mm. in diameter, and was probably five or six years old, possibly more. To all appearances the bark is smooth, but microscopically it is somewhat rough, the roughness due to the dome-shaped projections which occur over the stomatal chambers. The flowers are borne along the sides of very small sharp thorns. They have the appearance of being in a raceme—an umbel-like raceme, some authors call it. The leaves, said to be scalelike, are soon dropped.

INVESTIGATION.

The study of the desert plants was taken up in February, 1909, in connection with other graduate work at the University of Kansas, and continued until the middle of August of that year.

The methods employed in pursuance of this study were various. The chlor-zinc-iodide treatment of sections fresh from the formalin or paraffin, or softened from the dried state, proved on the whole the most satisfactory.

All the figures, except a few of the flower and some diagrammatic ones, were made by the aid of the camera lucida, the projection lantern or the photographic camera.

Stem.—The stem as a whole shows some interesting features in cross section, of which the thick epidermis, deeply sunken stomata, the deep palisade tissue, compact wood and small water tubes are not the least striking.

The *tissues* might be taken in their order, beginning with the innermost one. It has been observed that no generalization

can be made in regard to the structure of these desert plants, each one having its own peculiar way of getting on.

The *pith* occupies a sort of triangular area. The cells are comparatively large (see table), are heavily lignified, deeply pitted, stored with starchy material, and possessed of—in almost every case—a small crystal having the form of the calcium oxalate crystal. In the younger flower branch we find cells with thick walls, also, but retaining their rounded shape, pitted, and plentifully surrounded with air spaces. No food material was observed stored in this region. In the older stem elongated pit cells next the trachial tubes are densely filled with material that stains blue with c. z. i. This has a fine granular appearance (fig. 2, plate XX).

The *medullary rays* are conspicuously broad in cross section, many being five cells wide. The cells are comparatively large. They have the ordinary cylindrical shape with thick lignified and pitted walls. (Figs. 3 and 5, plate XIX.) Intercellular spaces are frequent. Most of the cells are full of non-nitrogenous material, while a few narrow and elongated ones appear adapted for quick conduction. Those between the phloëm strands show the characteristic proteid reaction with c. z. i. and have the usual unpitted walls. Crystals are often found in these cells.

The *xylem* makes up a great part of the stem. The wood fibers cannot be said to be very numerous. They have the usual shape and are rather short. (See table.) The fiber-tracheids are found quite plentifully and correspond closely to the wood fiber. The bordered pits, however, are very numerous, there being at least 200 to a tracheid. (Fig. 15, plate XX.) The pits are small. The spiral tracheids have the single and double spiral threads. These vessels are decidedly small. The tracheids are of three kinds and vary in length and diameter. (See table of measurements.) The tracheal tubes have many small bordered pits and have thickenings in ridges in the walls. The whole tube is divided at more or less regular intervals, as from 0.6 to 0.27 mm., by thick rings. Upon investigation these may sometimes be seen to be in the plane of union of neighboring tubes, the walls being so completely fused as to obliterate all trace of joining. It seems that these rings are really the borders of an aperture in the ends of tube elements, occurring in the earliest laying down of the tissue. They were observed in the last vessels laid down before col-

lecting in the midst of the rainy season of 1908. (See figs. 5 and 6, plate XX.) These pitted vessels, often with ragged inner thickenings (fig. 6), are found from the spiral vessels next the pith to the latest growth. They are also found in the young thorn which bears the flowers. The end of this division of the tracheal tube is often very much elongated and gradually tapering (figs. 3, 4, 9). Sometimes the long tapering is omitted and we have a peculiar cell ending as in figures 6*a* and 7. These elements sometimes taper at both ends, but frequently and abruptly in horizontal base. (Fig. 3.)

Besides the tube elements just described, there are the more or less rectangular tracheids that join their neighbors above or below by horizontal or oblique walls. (Fig. 13.)

No means to be had will give an exact account of the age of the stem. This is true of most of the perennials of the desert, we believe. Upon projecting upon the screen by means of the lantern, a cross section of the older stem showed traces of five or six seasons' growth, a slight increase in the size and number of the vessels being noticeable in each successive yearly growth as well as a somewhat greater compactness of growth in the wood itself. Probably for the year 1907 a new set of vessels has been formed. (Fig. 1, plate XVIII.) Outside of these is a second set of larger and unquestionably new water vessels laid down at the beginning of the rainy season of 1908. The width of an annual ring varies somewhat, but on the whole has an average of about 0.2 mm. The entire radial measurement of the wood from pith to phloëm is about 1.5 mm. This would make the stem about seven and a half years old.

The *Phloëm* region shows the usual storage of nitrogenous materials in the sieve and companion cell portion and in the parenchyma. The elements of the sieve vessels are rather long (see table) and full of fine granular material. The sieve plates are heavy, with very minute perforations on the sides. The phloëm parenchyma in my material occurs in a series of five parts, each being about three cells wide. (Fig. 1, plate XXI.)

The *stone cells* and *bast* make a hard, rigid cylinder around this more delicate portion, the stone cells occurring between the bundles of bast and extending around them.

The sclerenchymatous or stone cells are of various shapes: some are squarish, some oblong, and some so elongated as to be confused with the bast as far as shape goes, but possessing the deeply pitted characteristic of the stone cell. This zone

occupied by the stone cells is broad. Sometimes the cells are found in the region of the palisade cells, in scattered patches, or in many cases filling up air cavities below the stomatal chamber. (Fig. 1, plate XXIII.)

The bast appears to be of twofold character—the ordinary long, tapering cells, united by a long splicing, then another kind, shorter and tapering abruptly at one end, while the other end, rather blunt, fits securely into the socket made by the two cells below. (Figs. 8, 9, 10, plate XXI.) These fibers occur in the regular bundles, but they also make a sort of inner bundle, we think; at least, in all the cases so far examined they appear to occupy that position. They may make a sort of inner supporting shaft to the whole group. When separated from the long fibers a bundle of them looks like a barbed shaft.

The *spongy parenchyma* tissue takes up the inner collenchyma region. These are about five or six cells deep radially. The walls of some of the parenchyma of the innermost portion are heavily lignified. Neighboring cells have not so changed materially, but the cellulose wall is thicker in many cases. The walls in all the sponge are about twice as thick as those of the palisade region. The spongy cells are spherical, cuboidal or ovoid in shape, and about twice the diameter of the palisade cells. The numerous and large intercellular spaces in this region are conspicuous. There are besides whole rows of open spaces, seen in either cross- or longi-sections. (Fig. 9, plate XXII.) This will be taken up in a later paragraph, however.

The *palisade cells* lie in characteristic position, two or three deep radially. They are thin walled, cylindrical in shape, with some, but rather small, intercellular spaces. The chloroplasts are of goodly size, and show a deep blue in treating with c. z. i. In this region also are to be found very large aerating chambers, ovoid in shape, connecting directly with the stomatal chamber above, and thence with the outer world. These are not quite so numerous as the smaller cavities mentioned in the sponge. (Figs. 3, 4, plate XXII.)

The *epidermis* is remarkable. The cuticle itself is very heavy, it being 0.015 mm. in thickness in the old stem. The whole epidermis as found in the older stem measures from 0.075 mm. to 0.105 mm. There is but one row of epidermis cells. These are elongated radially, and in the younger parts of the plant are of thin cellulose walls. In the older parts the walls become very much thickened, so much so that in time only

a conical space at the bottom represents the cell cavity. (Figs. 4, 5, plate XXII.) At intervals these picket-like cells give way to large cavities, which they surround and protect by a slight modification at the outer extremity, a curving upward and inward, thus making a little dome of from eight to a dozen cell tips. (Figs. 3, 1, plate XXIII.) These, not entirely closing the cavity, leave an aperture allowing of communication between the outer world and the stomatal apparatus within and thence farther beyond to inner tissues. (Fig. 8, plate XXII.) The details of this arrangement, although seemingly complex, are actually simple. The stoma lies at the base of the epidermal air chamber; slight projections of the walls of the guard cells make a shallow stomatal chamber immediately above, and like ones make one below. Beyond the lower lies the large ovoid cavity referred to in the palisade tissue. (Figs. 8, 9, plate XXII, fig. 11, plate XXIII; and for measurements, see table, p. 7.) A curious little Phycomycete makes its home in the outside stomatal cavities. It occurs in a majority of the stem stomata. (Fig. 7, plate XXII.) There are about 150 stomata to a square millimeter. (Fig. 2, plate XXIII.) In the younger stem a tissue for water storage occurs just outside the pericycle. Sometimes this appears to be represented by a single cell only. (Figs. 8, 9, 10, plate XXIII.) The region of spongy parenchyma here stains deep blue with c. z. i., while the palisade cells remain yellowish.

Flower.—The flower, cream color to yellow, shows the four-parted arrangement—four very short triangular sepals, greenish in color; four long, blunt, prominently veined petals, enclosing eight stamens, which show an inequality in length of filament. The anthers are elongate-ovoid, and open on the side. They are attached to the filament at about one-fourth the distance from the base. The filaments are stout and tapering upward. The superior ovary is globose in shape, tapering above into a pillarlike style, which in turn tapers slightly at the apex to form the stigma, which is a plain surface surrounding a circular orifice.

Upon sectioning the ovary longitudinally the numerous ovules are noticed in longi-section; they appear hanging down from the central placenta. In cross section two cells are seen, and in some parts a suggestion of two side partitions. The ovary wall is cutinized heavily without and within, insuring

protection for the ovules against the intense aridity of the desert atmosphere. The mesophyll of the ovary is well supplied with chorophyll bodies and contains numerous mucilage cells, thus assisting in the provision for intensest drought. A resinous gum is found in the seed vessel surrounding the ovules and the vascular bundles in the placenta. (Figs. 1, 2, 3, 4, plate XXIV.) The resinous gum is not found elsewhere.

The contents of the cells of the stomata of the inner wall of the seed vessel stain a deep blue with c. z. i., showing that the guard cells here are living and filled with non-nitrogenous material.

The mucilage cells finally break down, thus forming large mucilage reservoirs. (Figs. 8, 7, 5, plate XXIV.)

CONCLUSION.

Koeberlinia is what Clements would call a stem xerophyte. The low stature of the plant, its compact habit of growth and the heavily cutinized surface everywhere, reduces evaporation to a minimum. The dead-air spaces furnished by the outer stomatal chambers also contribute toward this end. A supply of moisture is insured for the more strongly growing parts by the storage of water in special reservoirs and by the presence of mucilage in the seed vessel. The resinous gum aids in conserving moisture. Greater strength is secured, perhaps, through the peculiar splicing of the large tracheids. The stone cells, with their firm adherence to the bast fibers, also give strength. The air spaces in epidermis, palisade tissue, sponge, medullary rays and pith insure a goodly supply of CO_2 without much evaporation. These points might be summed up thus:

Evaporation minimized by:

1. Dispensing with leaves.
2. Heavy cutinization on all exposed surfaces.
3. Dead-air spaces (outer stomatal chambers).
4. Low stature.
5. Compact growth.
6. Resinous gum surrounding tender growths.

Moisture supply provided for by:

1. Special reservoirs for water storage.
2. Mucilage in cells in seed vessel.
3. Tracheal elements.
4. Presence of resinous gum.

Strength attained by:

1. Extreme lignification.
2. Long splicing of bast.
3. Long splicing of large tracheids.
4. Heavy zone of stone cells firmly adhering to bast.

Supply of air provided for by intercellular spaces in:

Epidermis.
Palisade.
Sponge.
Medullary ray.
Pith.

On the whole, this plant presents a wonderful array of "aids" to getting on in the desert. No other plant examined showed so thick an epidermis and such an aerating system. A few were almost leafless, a few had a heavy epidermis, some were strongly lignified, others showed resinous secretions. Almost all had larger water-conducting vessels. With all the adaptations that this plant had it seemed strange that it was so rare, but upon investigation we find that by abortion the many seeds are reduced to one, two or three to a berry. We have not yet found out whether the berry is eaten by animals or not.

Tables of measurement, rainfall and evaporation are presented for reference; also, a very superficial table giving some facts in regard to a few other desert plants. I am indebted to Mr. Peace for the tables on rainfall and evaporation. He has also kindly furnished the two photographs as well as much valuable information. Thanks are due to Doctor Trelease, Doctor Land and Doctor Spalding, for kindness in answering inquiries. I also wish to thank Doctor Billings for suggestions, and Professor Stevens especially for ever-ready assistance. It is a pleasure here to express gratitude to Doctor MacDougal for freely granting the facilities of the desert laboratory while the materials were being collected.

TABLE OF MEASUREMENTS.

	Structure.	*Length, mm.*		*Width, mm.*	
1.	Mid pith cell	0.03	to 0.045	0.03	to 0.075
2.	Marginal pith cell	.045	.075	.01	.015
3.	Medullary ray cell	.05	.075	.012	.014
4.	Wood fiber	.....	.24	.....	.....
5.	Fiber tracheid	.....	.25	.....	.015
6.	Tracheal tubes	.06	.27	.01	.03
7.	Tracheids	.....	.114	.015	.025
8.	Sieve cell	.03	.25	.....	.015
9.	Phloem parenchyma	.022	.12	.....	.015
10.	Stone cell	.05	.12	.015	.06
11.	Bast (long)	.06	.15	.....	.013
12.	Bast (short)	.015	.03	.....	.007
13.	Spongy parenchyma	.015	.03	.....	.02
14.	Palisade cells	.....	.....	.01	.012
15.	Epidermis, older stem	.....	.....	.075	.105
16.	Cutinized portion epidermis, old stem	.....	.....	.....	.075
17.	Epidermis flower branch	.....	.....	.....	.06
18.	Cutinized portion epidermis, flower stem	.....	.....	.....	.013
19.	Epidermis-ovary, outer	.....	.....	.03	.065
20.	Cutinized portion epidermis-ovary, outer	.....	.....	.01	.015
21.	Epidermis-ovary, inner	.....	.....	.02	.045
22.	Cutinized portion epidermis-ovary, inner	.....	.....	.....	.01
23.	Epidermis of anther	.....	.....	.....	.02
24.	Cutinized portion epidermis, antner	.....	.....	.....	.0019
25.	Epidermis of petal, outer	.....	.....	.....	.02
26.	Cutinized portion epidermis-petal, outer	.....	.....	.....	.0019
27.	Epidermis petal, inner	.....	.....	.....	.015
28.	Cutinized portion epidermis-petal, inner	.....	.....	.....	.0019
29.	Upper stomatal space	.....	.12	.....	.04
30.	Lower stomatal space	.....	.06	.....	.03
31.	Outer stomatal aperture	.....	.....	.....	.008
32.	Inner stomatal aperture	.....	.....	.....	.015
33.	Air space in sponge	.03	.045	.025	.032
34.	Mucilage cells	.....	.....	.....	.0325
35.	Mucilage reservoirs	.....	.....	.06	.15
36.	Water storage cells	.03	.06	.03	.045
37.	Resinous gum cells	.03	.092	.015	.02
38.	Intercellular space, pith	.....	.....	.007	.015
39.	Intercellular space, sponge	.....	.....	.003	.015

RAINFALL NEAR TUCSON.

Jan. 3	0.62 inch.	Apr. 23	0.11 inch.
" 15	.05 "	May 3	.05 "
" 23	trace.	" 23	.03 "
" 30	"	July 5	trace.
Feb. 3	0.29 inch.	" 7	0.04 inch.
" 4	.57 "	" 10	trace.
" 7	trace.	" 13	"
" 10	0.16 inch.	" 15	0.80 inch.
" 11	.47* "	" 16	1.00 "
" 13	.24† "	" 17	2.6 "
" 22	.15 "	" 19	.01 "
Mar. 4		" 23	.61 "
" 19	trace.	" 25	1.81 "
" 20	0.38 inch.	" 27	.02 "
" 26	.03 "	" 28	.42 "
" 27	.01 "	Aug. 2	.42 "

* With snow. † With sleet and snow.

TEMPERATURE AT THE DESERT LABORATORY.

	Lowest.	*Highest.*		*Lowest.*	*Highest.*
July 6	77° F.	99° F.	July 18	65° F.	74° F.
" 7	77	103	" 19	68	87
" 8	74	99	" 20	75	95
" 9	78	90	" 21	75	99
" 10	78	95	" 22	75	94
" 11	74	101	" 23	62	92
" 13	71	100	" 24	65	90
" 15	67	97	" 25	72	91
" 16	69	88	" 26	62	92
" 17	64	82	" 27	69	84

RAINFALL OF TUCSON VICINITY.

	1904.	1905.	1906.	1907.	1908.
January	....	1.91	0.60	2.47	0.67
February	....	4.11	1.26	0.08	1.89
March	....	4.27	0.31	0.41	0.52
April	....	3.11	0.34	0.00	0.11
May	1.29?	0.03	0.02	0.45	0.08
June	0.04	0.24	0.00	0.00	0.00
July	2.07	1.47	2.07	4.67	5.73
August	3.00	0.47	1.16	3.66	*0.42
September	0.61	2.24	0.28	0.28	....
October	0.07	0.05	0.01	0.95	....
November	0.05	4.52	0.66	0.74	....
December	1.07	0.90	4.40	0.00	....
Totals	8.20	23.31	11.10	13.72	9.42

* To August 2.

From July 5 to July 31 there were twelve days upon which rain fell. There was rain during one day of each of the months of April, May and June. (These statements apply only to the year 1908.)

WEEKLY AVERAGES OF EVAPORATION,

In cubic centimeters, from free surfaces at a height of 25 centimeters above the ground.

	June.	July.	August.	September.
Tucson	338	228	212	278
St. Louis	112	157	140	137
Lincoln	96	90	113	144
Chicago	93	95	109	95
New York	...	48	63	35

Temperatures, July 5, 1908, to August 2, 1908: Lowest, 62° F.; highest, 103° F.

NAME.	Epi.	Pith.	Water tubes mm. × sec.	Wood.	An. ring.	Med. ray.	Bast.	Air space.	Storage.	
									Food.	Water.
Cassia covesii.....	Thin.	0.0015	0.03 even scat.	Dense.	'08 only.	1 cell wide.	Bundle.	In pith.	Rays.	
Celtis reticulata		0.007	0.045	Dense in patches.	0.45 mm. '07; prominent.	?	Narrow ring.		Pith.	
Cercidium torreyana.....		0.003	0.037	Dense mod.	0.07 mm. few; '06.	1 cell wide.	Bundle.		Pith.	Epedemics.
Covillia tridentata.....		0.006	0.05 to 0.015	Dense.	Slightly marked.		Heavy band.		Rays tracheids and pith.	Epidermis.
Encelia farinosa.....		0.0015	0.045	Trach. 0.001	0.27 mm.; plain.		Bundle.		Few pith.	
Fouquieria splendens....	Cells many.	0.0015	0.04	Fibers.				Frequent pith.		?
Jatropha.....		0.0015	0.06	Trach. only 0.05	0.6	1 cell wide.		In pith.	Rays—pith.	?
Koeberlinia spinosa.....	0.09 mm.	0.007	0.004 to 0.015	Dense fib.—trach.	0.21 mm. '07; prom.	2 to 5 cells wide.	Bundle.	Bark.	Rays—pith.	
Krameria	0.029	0.0025	0.03	Dense fib.—trach.	0.38, '07—0.6	1 cell wide.		Minute.	Pith.	
Phoradendron	0.022	0.003	0.03 to 0.015			Immense.			Everywhere.	
Parkinsonia microphylla,	0.007		0.06 to 0.09	Trach. 0.014	0.45 mm.; 9 yrs.	1-3 cells wide.			Pith.	
Prosopis velutina.....		0.005	0.07 to 0.015	Heavy in patches.	0.3 (?)	1 cell wide.			Tracheids.	
Sambucus.....	Sev. celled.	0.0015	0.037	Few fib. trach.	'07—0.37 mm.	1-3 broad.	Bundles.	Few large.	Trach. rays.	
Schinus mollis.....			0.03	Trachs. mostly.		Row large.	Little.	Few large.	Rays.	Bark.
Negundo sp.....		0.0015	0.045 to 0.015	Tracheids.	0.3 to 0.15 mm.	1 cell wide.	In bundles.		Rays and pith margins.	

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CONTENTS:

A Case of Absolute Tone Memory, ... *Archibald Hogg.*

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A CASE OF ABSOLUTE TONE MEMORY.

BY ARCHIBALD HOGG.

EXTRAORDINARY forms of consciousness are necessarily few, otherwise they would not be extraordinary. They are usually worthy of study and report directly by reason of inherent interest and indirectly through the light they throw on mental process in general. Among the exceptional forms of memory activity we find in hearing what is called by musicians "recollection of absolute pitch," by psychologists "absolute tone memory." A striking instance of the possession of this faculty led the writer, assisted by a friend[1] who is a skillful amateur violinist, to make the two tests herewith reported.

The subject[2] is a boy thirteen years of age, a quiet, gentle lad, imaginative, introspective, fond of his music and of long walks, and is perhaps less vigorous than the average child of the same age.

He gave early evidence that he possessed unusual musical gifts. One night when he was about four years old, and while lying in bed, he listened to the playing of a wedding march at a marriage ceremony in a neighbor's house. The next morning he climbed on the piano stool at home and reproduced the march—but in a simpler way. At the age of six his musical education began with lessons on the piano, and it has continued ever since except when interrupted by the vacations and illnesses incident to childhood. His possession of absolute tone

1. Mr. A. K. Hubbard, assistant professor of civil engineering in the University at the time.

2. The boy is the son of a professor in our University. Both parents are musical. One older brother plays the cello, another plays violin. Two younger children cannot be characterized with much certainty yet with respect to musical ability.

memory was so strikingly emphasized as to attract attention one day about three years ago, when he remarked to an older brother who had just tuned a cello that the pitch of the instrument differed from that of a few days before—an observation that was verified by appeal to the piano. Since then the boy has been tested, usually for amusement or out of curiosity, some five or six times, but without any records being kept. Composition comes easy to him and he has composed not a few melodious pieces during the last four or five years.

The notes given in the tests and the observer's judgment are indicated in accordance with a quite simple plan. The notes from and including middle C to its octave above are left unmarked. A tone in the next higher octave is indicated by a single accent mark above the letter, in the second higher by two accents placed above, and so on; similarly with the lower octaves, except that the accent marks are placed below the letter in such instances. The usual symbols for sharp and flat are used after the prescribed fashion.

The note or notes struck are placed first in the record and are followed immediately by the observer's judgment. In both tests the observer himself was seated with back turned at a distance of about eight feet from the instrument and was looking away from it. In other and unrecorded tests at home he has been sent at different times to various places about the house within hearing distance of the piano. The results of the unrecorded tests have been practically the same, as conversation with people present on such occasions has revealed. The uniformity of testimony regarding these unrecorded tests is the reason why more tests were not made by the present experimenters.

The first test was made on the observer's piano in April of this year. The results are given in table I.

Several times the observer was asked not to name the notes but to come to the piano and point them out without striking the keys. It was doubtless an unnecessary precaution.

A few miscellaneous tests were next made. The observer was asked to reproduce, either by whistling or singing, certain notes that were named, and thereupon sang or whistled in correct pitch, as shown by the piano, the following notes,

$$f\sharp', \ g\sharp, \ c\sharp_{/}, \ b\flat, \ f, \ b''' \ a'', \ d$$

Following that a simple tune was played on the violin and the key asked for. It was promptly and correctly given. The

TABLE I.

Stimulus.	Judgment.	Stimulus.	Judgment.
C	C	$D_{,}$	$D_{,}$
E	E	F B♭	F B♭
A'''	A'''	$B_{,}$ G	$B_{,}$ G
D''	D''	G G♯	A♭ A
$B_{,,,}$	$B_{,,,}$	$E_{,,,}$ $G_{,,,}$	———
G'	G'	B''' F'''	B''' F'''
$F_{,,,}$	$F_{,,,}$	$G_{,,}$ $B_{,,}$ $D_{,}$ $G_{,}$	$G_{,,}$ $B_{,,}$ $D_{,}$ $G_{,}$
B'''	B'''	$E♭_{,,}$ $G_{,,}$ $B♭_{,}$ $D_{,}$	$E♭_{,,}$ $G_{,,}$ $B♭_{,}$ $D_{,}$
$D♯_{,,,}$	$D♯_{,,,}$	C F♯	C F♯
G'''	G'''	$E_{,,,}$ G'''	$E_{,,,}$ G'''
A♭′	A♭′	$D_{,}$ C♯	$D_{,}$ C♯

experimenters having an idea as to the method of recognition, parts of three or four tunes were played, care being taken not to stop on the key note. The recognition was again prompt and accurate. Being questioned, the observer said his judgment in the first instance was determined by following the general rule that a simple melody ends with the key note. In the subsequent selections the judgment was determined by the sequence of the notes.

Then a high note on the violin between b♭″ and b″ was struck. When asked the pitch the observer mentioned b″, and upon being told it was not exactly that he named b♭″.

Next, several double stops were given on the violin, one note being a shade off the key in each case. The note that was in error and the direction in which it should be changed were correctly given. The observer was now asked to direct the operation of tuning the A string of the violin until it corresponded with his own piano. The result, as shown by the piano, proved that the judgment was slightly in error in the flat direction. The same test on the D string gave a correct judgment. Practice with the A string doubtless helped here.

Lastly, the opening notes of a piece were sung. They were named correctly by the observer, as appeal to the piano demonstrated. He is ignorant of fingering of the violin.

The second test was made one afternoon about a month later with the piano used twice a week by the observer when he

takes his music lesson. The instrument is tuned to international pitch and is lower than his own. He said it sounded flat. The results are in table II.

TABLE II.

Stimulus.	Judgment.	Stimulus.	Judgment.
C♯	C	G‴	G‴
G_{III}	G_{III}	A♭′	G′
A‴	A‴	D_{I}	D_{I}
D″	D″	A♭′	G′
$B♭_{III}$	$B♭_{III}$	G♯‴	G‴
G_{I}	G_{I}	F B♭	E A
B♭	B♭	$B♭_{I}$ G	A♯, F♯
D♯‴	D‴	C F♯	B F
F♯‴	F‴	G_{II} B_{II} D_{I} G_{I}	G_{II} B_{II} D_{I} G_{I}
F_{III}	F_{III}	G♯″ B♯″ D♯‴ G♯‴	G″ B″ D‴
B‴	B‴	G″ B♭″ D″ F‴	F♯″ A″ C♯‴
$D♯_{III}$	D_{III}	E♭ G B♭ D	D F♯ A C

With the first of the errors it occurred to the experimenters that the judgments were being determined exclusively by simple comparison with the image-standards from the home piano—an hypothesis which would have involved uniformity in the errors. Notes a half tone lower in pitch than those really given should have been named.

Later it occurred to us that the observer himself might be trying to correct the difference between the two pianos. That this was usually the case became known from answers to questions asked after the test. The observer arrived at most of his judgments by traveling the following mental highway: The tone was first identified and named by means of the images from his own piano—the instrument on which he daily played and with which his familiarity was great. Having thus identified the tone as nearly as possible (exact correspondence in any instance would be highly improbable), the simple addition of a half tone brought about the judgment announced.

In a few cases direct recall of the tone-images from the teacher's piano rendered any additional mental labor unnecessary to identification.

In closing, a few statements are made by way of addition and partial summary. For our observer the difficulty of identifying a single tone is scarcely harder in one region of the piano scale than another. But there is a decided difference in ease of analysis according as there are high or low complexes of tones. In the third octave below the mental separation of two notes was not attempted, the remark being made, "It's such a jumble, I can't remember," while in the third above the identification was made with accuracy and without a noticeably great amount of concentration. Images from the organs of utterance seemed to play no part whatever in his recall of tones. Sound images apparently furnished exclusively the material used in all the judgments. Upon being questioned as to his method of identification and of reproduction the observer said he "just heard the tones in his head and told in that way." Of a piece of music recently purchased for him he said he had played it off "in that way" before touching a finger to the piano. His introspective competency was greater than was expected.

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CONTENTS:

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THE HACKBERRY PSYLLA, PACHYPSYLLA CELTIDIS-MAMMÆ RILEY.

A STUDY IN COMPARATIVE MORPHOLOGY.

BY H. B. STOUGH.

Plates XXVI to XXXV, and three figures.

(Contribution from Entomological Laboratory, No. 158.)

Submitted in partial fulfillment of the requirements for the degree of Master of Arts.

OWING to their minute size and obscure life habits, the members of the homopterous family Psyllidæ have received comparatively little attention in North America. In the present paper an endeavor will be made to add to our knowledge of this family, using as a type *Pachypsylla celtidis-mammæ* Riley, the same being a study in comparative morphology of mouth parts, thorax, and genitalia, and development of wing venation and wing pattern. The specimens upon which I have based my studies emerged from their galls upon the hackberry trees during October of 1908, at Lawrence, Kan. I wish to thank Prof. S. J. Hunter, upon whose suggestion the problem was taken up, and under whose guidance and counsel the work was carried on, for his interest in my investigations and for his assistance rendered.

In search for literature on the Psyllidæ of North America, and especially that dealing with *Pachypsylla celtidis-mammæ* and its genus, I was impressed with the fact that very little of a definite and final treatment has ever been given to these insects in this country. A few species have been described, a few figured, and the life histories of a number worked out, while keys for the species of only about one genus can be found.

In Europe, on the contrary, the contributions to the knowl-

edge of this family have been numerous and have added greatly to our information on the subject. The first of these contributions was made by Förster, in 1848. He was followed by Flör, Thomson, and Hartig, but not much of an advance was made upon Förster's work until there appeared in 1879 a treatise, "Zur Systematik der Psylliden," by Löw; this, together with other contributions by the same author, has long remained authoritative. The researches of Löw in the taxonomy and biology of the Psyllidæ, together with the anatomical work of Witlaczil, have much simplified the study of this family in Europe.

James Edwards, in "Hemiptera-Homoptera" (1896), treats of four genera of the family, including twenty-eight species of British Psyllidæ, with tables for the separation of the genera and species. He also illustrates these forms in color and gives the typical wing venation of each genus.

Maskel (1889) lists and describes four species of Psyllidæ from New Zealand, giving keys for separating the subfamilies represented in that locality, and figures the larval, pupal and adult stages, and some of their typical anatomical characters. This paper contains more figures of these characters than any other I have been able to find, and was quite useful from that standpoint. This writer also discusses the use and taxonomic importance of the different characters of the family.

Froggatt (1903), in a paper on "Australian Psyllidæ" describes eighteen species, mostly of the two genera *Aphalaria* and *Trioza*. He figures the galls made by three species of the latter genus.

The reasons for the dearth of material in this country may be found in the fact that the family Psyllidæ, like some other little-known groups, being composed of small and inconspicuous insects, has not been largely collected and studied, two or three species excepted. One of these, the pear Psylla, *Psylla pyricola*, is of great economic importance in some localities, and has long been known and its life history carefully worked out. The life histories of these insects are very difficult to determine definitely, and since some of them are gall-formers, the biological side of the work becomes still more complicated. Only about three specialists have ever devoted much time to their study in this country, among whom was C. V. Riley. In an article on "The Psyllidæ of the United States" (1883), he gives a *résumé* of the present knowledge of the family and its principal char-

acters, habits, life history, etc., listing thirteen species. Undoubtedly the most important work published so far is that by the same writer entitled "Notes on North American Psyllidæ" (1884). This paper lists nineteen North American species, distributed among the following genera: *Livia, Aphalara, Psylla, Pachypsylla, Trioza, Calophyla, Rhinopsylla,* and *Ceratopsylla,* the descriptions of three genera and two species being new. The most important part of this work, from the standpoint of the present paper, is that dealing with the new genus *Pachypsylla.* This genus is peculiar to this continent, having no equivalent in Europe, so Riley thinks, and to it belong the hackberry psyllids. Only three species of these are placed in his key. Riley also discusses "hackberry galls," in the *Canadian Entomologist* (1883).

An important contribution to the biology of the subject, especially of the gall-making phase, is an article on psyllid gall-making in the fifth report of the United States Entomological Commission, written by A. S. Packard (1887). This gives keys to three species; descriptions of pupa; key to, and descriptions of, the galls of the following species and varieties of the genus *Pachypsylla: venusta, gemma, asteriscus, umbilicus, mamma, pubescens, globulus, cucurbita,* and *cucurbita var.* To this is added a detailed description of each gall and a condensed general life history of a hackberry psyllid. No mention is made of the stimuli causing the gall-formation. Ashmead (1881) describes the life histories and gall-making habits of these insects, and lists nine species, adding three new ones.

Two papers by Charles W. Mally, entitled, respectively, "Hackberry Psyllidæ Found at Ames, Iowa" (1893), and "Psyllidæ Found at Ames" (1894), give a series of observations on the winter habits and spring egg-laying of *Pachypsylla celtidis-mammæ,* with descriptions of the eggs, larvæ, pupæ, and galls, and record thirty-one species for North America. He describes four new species and figures the early stages and wing venations.

Where mention is made of the galls in the papers that I have mentioned, only the gross structure of the gall is treated. Cook, however, in "Galls and Insects Producing Them" (1903-'04), has made a contribution toward the histology of the psyllid gall; he also discusses mouth parts and ovipositors in their relation to gall-formation, but in common with other investiga-

tors was not able to add much to our knowledge of the gall-producing stimuli.

On the mouth parts of Hemiptera, in addition to works of a general nature, I would cite two of importance in throwing light upon the homopterous mouth as seen in the Psyllidæ. These are by Charles L. Marlatt (1898) and Walter J. Meek (1903), and deal with the mouth parts of the cicada. Besides these, such works as those of Sanborn on the Aphididæ (1905), Berlese on Coccidæ (1896), and others, were of use in a comparative study. The best work upon mouth parts of Hemiptera is recorded in the German of Leon (1887), Geise (1883), Wedde (1885), and Heymonds (1899). Dohrn (1865) contributed to the internal anatomy of the Hemiptera, and Witlaczil (1885) worked out the brain, eyes and digestive system.

GENERAL CHARACTERS OF THE FAMILY PSYLLIDÆ.

The Psyllidæ were formerly classified with the Aphididæ, to which they are closely related, and are still sometimes known as "the jumping plant lice." These insects are from one-eighth to one-fifth of an inch long and in general appearance may be likened to a minute cicada. Their principal characters follow: Hind legs developed for jumping; antennæ nine- or ten-segmented (in life in constant vibration), last segment bearing two short spines; tarsi two-segmented; mouth parts suctorial; wing venation comparatively simple. Some of the species are of economic interest, being injurious through their feeding habits. A number form galls, notably upon hackberry. A few species secrete "honey dew."

According to Mally (1894) there are thirty-nine species and varieties in North America. Only nine species are to be found in the collection of the University of Kansas, four of these having been taken in Kansas. So far, not many fossil insects of this family are known. Scudder lists in "Tertiary Insects of America" (1890) only two species, *Necropsylla rigida* and *Catopsylla prima*, the latter being of interest, as its wing venation resembles more closely that of Riley's genus *Pachypsylla* than of any other.

The species taken for study belongs to this last genus, *Pachypsylla*. The namer, C. V. Riley, says of it: "There is no genus among those characterized by Dr. Fr. Löw with which

Pachypsylla can properly be compared. In the convexity of the body it greatly surpasses *Psylla,* from which it is at once distinguished by the vertical and rugosepunctate head, the quadrate vertex, the short frontal cones, the less filiform and stout antennæ." This species was first listed for Kansas by Tucker in 1907.

The coloration of *Pachypsylla* has been well described by Riley. The general color is dark brown, with the abdomen showing pinkish shades along the edges of each segment. The wing pattern is dark brown, and the ocelli are red.

This insect is quite short bodied; the sexes are easily distinguished, as in all representatives of the family, the end of the abdomen being pointed in the female but blunt and appendage-bearing in the male. The total length of body averages, for the male, 3.2 mm., and for the female, 3.6 mm.

HEAD.

The head is carried in such a position relative to the remainder of the body that the epicranium is in an almost vertical position (*34*-4),* the frontal cones pointing downward, with the outer face of the frons in a horizontal position, its distal end projecting caudad. Viewed from the front, the head corresponds roughly, in general shape, to a right triangle, truncate at the vertex, the posterior edge of the epicranium lying on the base of this triangle, and a point somewhat beyond the frontal cones representing the vertex (*28*-4). The whole head is rather flat, thin, rectangular, and boxlike, the open side of the box being the caudal side (*28*-1), against and into which opening fit the anterior part of the prosternum, the procoxæ and the mouth parts.

The following parts and regions of the head, excluding the frons and clypeus, which will be described under "mouth parts," are to be found: epicranium, genæ, frontal cones, antennal sockets, compound eyes, and ocelli.

The epicranium forms the front wall of the head and is vertical in position. Its posterior margin is slightly concave, and curves caudad and ventrad to the opposite side of the head, forming a roll-like edge. This roll-like portion is the dorsal part of the head when the latter is in normal position. This region of the head (*28*-4, *ep*) is rectangular, about 0.45 mm.

* Read plate XXXIV, fig. 4.

wide and 0.62 mm. long. Its posterior edge is concave, as are also the lateral edges which border on the compound eyes, while the anterior margin is quite convex and has a somewhat more than semicircular excision at its median point, in which region is located the frontal ocellus, seen in figures 4 and 5, *fo*, and in 2 in longitudinal section, pl. 28. The epicranium is seen to be flat in surface when the head is viewed in profile. The other two ocelli (*28*-4, *o*) are placed at the two posterior angles of the epicranium, near its margin and slightly posterior to the compound eyes. They are about 0.07 mm. in diameter. The epicranium is divided along its median line by a very plainly cut suture into two equal sclerites. This suture is deep, and in making dissections of the head these two sclerites were often separated readily along this line. The anterior, convex suture between the epicranium and the rest of the head was not so apparent in most specimens that I examined, though usually those boiled thoroughly in potassium hydrate and then carefully cleared in xylol showed it more plainly. The surface of the epicranium is rugose-punctate, slightly pubescent.

The frontal cones, erroneously called "cones of the clypeus" by Slingerland and "face lobes" by Scott,[1] are found, one on each side of the median line, below the epicranium (*28*-4, *fc*). As seen from the front (*28*-5) they diverge from the vertex just beyond the front ocellus. They are separated from the cheeks or genæ by a curved suture, which appears somewhat ovate when the cones are viewed from below. This suture could be made out much more easily on the cephalic than caudal surface of the head.

The genæ (*28*-1, 4, 5, *g*) extend from the cephalic edge of the epicranium down on each side under the compound eyes and fuse with the caudal, folded portion of the epicranium. Between the cones and the compound eyes is the antennal socket (fig. 5, *as*), which is quadrate in shape, with angles much rounded, and with a blunt projection, *p*, breaking into it on its caudal edge, which is concerned with the articulation of the basal segment of the antenna. The aperture filled by the prosternum, procoxæ, frons and mouth parts is similar in shape to that of the epicranium but narrower. On the edge of the gena, midway between the vertex and the compound eye on each side, is situated a sharp projection (figs. 1 and

1. Insect Life, vol. V, pp. 229-230.

5, *y*), forming the attachment for a membrane which runs caudad between the front coxæ, and which will be mentioned more fully later. The outline of the compound eye is somewhat more angular than rounded, viewed from either the front or the rear.

In my study of the sclerites of the head I have followed Comstock and Kochi, and my conclusions for *Pachypsylla* agree largely with the facts recorded by them.

ANTENNÆ.

The antennæ are filiform, rather stout (a characteristic of the genus *Pachypsylla*), and average 0.83 mm. long. They are 10-segmented (*28*-3). The relative lengths of the ten antennal segments on the basis of the length of the first segment may be represented thus: 1, 1, 2, 1.2, 1.1, 1.2, 0.8, 1, 0.7, 0.4; the second segment is wider distally than proximally and is distally notched; the fourth, fifth, sixth, seventh and eighth segments are constricted proximally; the tenth segment is the smallest segment and bears at its distal end two stout, blunt, diverging spines (fig. 12), which are about as long as the segment and appear to be hollow. The last few segments are compressed dorsally.

The cuticula of the first two segments is very deeply rugose, forming scales, which on the second segment become longer at the distal end (*28*-3). The surface of the remaining segments is covered with deep, transverse corrugations (*28*-6), which give to each segment a sharply serrate lateral edge, the teeth pointing distad. A fringe of sensory hairs is found on the distal ends of the segments, and a few scattered along their surfaces, the tenth segment being without conspicuous hairs. Figure 9, plate XXXIV, shows the last four segments, with their corrugations and the terminal spines, while figure 6, plate XXVIII, is of the articulation of the third and fourth segment, showing the sensory hairs and the cuticular structure.

MOUTH PARTS.

The suctorial mouth as found in the homoptera, and as described by Meek (1903) and others, consists of labrum, epipharynx, labium, hypopharynx, and setæ. These parts are all represented in *Pachypsylla*. Closely associated with them are the frons, clypeus, mandibular and maxillary sclerites, and tentorium, corresponding in position to those in the cicada.

These parts are so closely associated with the mouth parts proper (labium excepted), forming as they do a distinct region of the head, which is torn loose in dissection as a single complex of sclerites (*32*-1), that they will be described in this connection.

On account of the vertical position of the epicranium, the mouth parts assume an orientation by which the frons, clypeus, and labrum are almost horizontal, their distal ends projecting caudad (*28*-5). The basal portion of the labium has a similar orientation, but distad of its bend (*29*-2) it observes a general ventral direction, though possessing some latitude of movement cephalad and caudad.

Frons.—The frons is the largest and heaviest sclerite in this region. Viewed from in front (looking dorsad) it is seen to be obovate in outline (*29*-3). Viewed from the side (fig. 1) its ventral outline is strongly rounded basally, with a dent at about the beginning of the distal third. Its basal edge is thickened (figs. 5 and 1) and continued laterally into processes (figs. 5, 3 and 1) which join the lateral ends of the rod-shaped tentorium, *t*, and the chitinized rods, *cmx*. At the place where the rods *xyz* (fig. 5) above mentioned leave the frons at *x*, same figure, there springs a ligamentary process (*28*-5, *lp*), which runs cephalad and dorsad of frons, forming a small plate above the latter, and this plate in turn is connected to the vertex by two small ligaments. These are for the attachment of the frons to the head, still leaving some opportunity for motion. The frons is rugose-punctate of surface.

Clypeus.—The clypeus (*29*-1, 3, *c*) is about one-third as long as the frons. It is more or less rectangular as viewed from the front, broader at proximal end, and its lateral edge is bent dorsad, thus partly enveloping the stylets or setæ. The slightly curved suture between this sclerite and the frons was clearly marked in most specimens examined, though in a few it was not readily discerned.

Mandibular and Maxillary Sclerites.—Between the lateral edge of the frons and the rod *cmx* (*29*-1), and bounded proximally by the arm of the frons which joins *cmx*, is a more or less circular foramen through which the bases of the setæ may be seen (figs. 3 and 1, *for*). This foramen is bounded distally by two sclerites; the proximal is crescent-shaped and is known as the mandibular sclerite (fig. 1, *mds*); the distal is

triangular and extends forward about as far as the end of the labrum and is called the maxillary sclerite (fig. 1, *mxs*). The end of this sclerite has a rather slender, curved portion at its apex, called the "maxillary process." These two sclerites are shown in figure 3 in ventral aspect, and in figure 1 in lateral aspect, where the clypeus, labrum, setæ, etc., have been bent ventrad in order to show the parts free and not overlapping. The edge of the maxillary sclerite and maxillary process are also shown in figure 5 looking ventrad. According to Smith (1892) these two sclerites represent the true mandibles and maxillæ, the setæ not being considered as such.

Mouth Parts Proper. *Labrum.*—The labrum (*29*-3 and 1, *lab*) is only about half as long as the clypeus and differs in shape from the labrum of the cicada in that instead of being a narrow, pointed process, it is, as viewed from in front, rectangular in general shape, slightly longer than broad, with distal corners rounded. It is not so flat as in the cicada, but its lateral edges are bent dorsad in the same manner as those of the clypeus, so as to partly surround the setæ and the pharyngeal canal. At the proximal end of the labrum is found a slightly curved suture between it and the clypeus. This suture was very hard to make out, and the two sclerites in some specimens appeared almost as if fused. Viewed from one side, the ventral outline of the labrum is seen to be slightly convex, with the distal portion bent somewhat ventrad. Marlatt's nomenclature makes the frons the clypeus and the clypeus and labrum a two-piece labrum.

Epipharynx.—Situated under the labrum (*29*-2, 3 and 1, *ep*), and shorter than the same, is an indistinct organ, the epipharynx. In the psyllid this organ is a delicate, fleshy, tongue-like structure, more or less triangular in shape, with a blunt tip, extending as a sort of outgrowth from, and extension of, the labrum. It appears as if it were a prolongation of the labrum, and it was difficult in most cases to determine where the one ended and the other began. The epipharynx is pressed tightly upon the upper surfaces of the setæ, surrounding them somewhat on the sides, and thus supplements the labrum in keeping them together to form a tube.

Labium.—The labium is attached below the hypopharynx, on the lower side of the head (*29*-1, *labi*, and *34*-6). This attachment is by means of a delicate membrane made fast to the

edge of the foramen next to the frons, which is easily torn away in dissection. At first the labium is merely a membranous band with only very slightly raised edges, which in this region of the organ are somewhat chitinized. These edges gradually become more raised and lose their chitinization until finally a little before the bend in the labium these edges become broad flaps which come together, and from this point to the tip there is left only a slit (*29*-4). The epipharynx lies naturally against the floor of the labium, but it can be lifted clear, together with the remainder of the parts, for some distance from this position. The first or basal segment of the labium is membranous, not chitinized, since it is so well protected between the procoxæ in a membranous fold. Each procoxa is placed very close to and almost fits the foramen laterad and dorsad of the frons (*29*-1, *for*). The first segment of the labium lies between the front coxæ, embedded in a membrane, and these coxæ almost meet over (ventrad of) it (*29*-2 and *31*-1).

The attachment of the labium to the prothorax, in this case to the region between prothorax and mesothorax, typical of the Homoptera, is very strong as compared with that between labium and head. In fact, in most cases when the head was removed from the rest of the body the labium remained fastened to the thorax but tore loose at its base from the head. Meek mentions such a condition as present in the cicada, calling the structure on the thorax to which the labium is attached a "collar," describing it in the following words: "A heavy membrane attaches the labium to a chitinized collar of the thorax." In *Pachypsylla* this collar is a chitinized process (*27*-4) embedded in the membranes between the prothorax and mesothorax (*29*-2, *p*). This process consists of two heavily chitinized structures, flattened and concave at their distal ends and large and swollen at their proximal ends, which are connected by a curved, chitinous rod as a sort of yoke, which is immediately under or dorsad of, and partly encircles, the labium just cephalad of its bend (*29*-4, *b*). The bases of this process are embedded in the membrane dorsad and somewhat caudad of the cephalic margin of the mesothorax, from whence the process projects ventrad and cephalad. The distal, parallel ends of these are roughened on their edges and hollowed out to form a groove, which, assisted by membranous

attachment, holds that portion of the labium just beyond the bend. Connected to the distal ends of these processes are membranes which run cephalad between the bases of the prothoracic coxæ, surrounding the labium, to form a sort of fold or groove for the same. This arrangement may be seen in figure 2, plate XXIX, in diagram, *m* representing the membrane surrounding the labium, *p* the process holding labium to thorax; the position of the labium and setæ may also be seen. Figure 1, plate XXXI, a cross section through the base of the mouth parts and procoxæ, corresponds roughly to Meek's "Fig. 13" for *Cicada*, and shows the great similarity between the two forms. The bases of the membranes surrounding the labium are here illustrated.

The labium is slitted throughout its entire length. At its base, where it is almost flat, it has only short, low, lateral edges or flaps, and hence is broadly open, and the upper parts of the mouth fit into this (*29*-2, 4). The labium, epipharynx and setæ all lie on the floor of the labium. Just at, or a little beyond, the end of the epipharynx the lateral flaps become larger and converge, their wavy margins fitting rather closely together. From here on to the end of the labium these flaps do not diverge again. Figure 6, plate XXXI, represents a cross section of the first segment of the labium just beyond its bend. Here the slit is seen to be held together by means of grooves and ridges. There is also a depression on its caudal wall. The lining of the labial canal is somewhat chitinized. On each side of the canal are found two longitudinal muscles, *m* of the same figure. The first labial segment is much roughened distally; the second is quite short, chitinized, and bears sensory hairs at its distal end; the third segment is heavily chitinized, with a pointed tip ending in two lateral, tonguelike processes. The lateral outline of these is seen in figure 2, plate XXXI, and in cephalic aspect in figure 3. The most notable feature of these processes is the three large sense organs on each—large spines on pegs. These same three sense organs are found on the labium of Aleurodidæ. This segment also bears several large sensory hairs, two of which are much longer than the segment itself.

Pharynx.—This is tube-shaped, chitinized, spreading somewhat at its cephalic end (*29*-5, *p*). Its ventral surface is supplied with eight pairs of muscles and tendons, which run

to the inner surface of the frons. At its distal end the pharynx fuses with the hypopharynx and hypopharyngeal lamellæ. The organ is heavily chitinized and thick-walled for some distance, but soon becomes narrower and, losing its chitinization, proceeds caudad until about the middle of the back part of the head, where it turns abruptly caudad and enters the thorax to become the œsophagus.

Mandibles and Maxillæ.—In dissecting the mouth parts the labium is generally torn loose from its connection below the hypopharynx and other parts and left connected to the thorax, as already mentioned. The setæ, however, remain fixed firmly to the upper parts of the mouth (*32*-1) and can be separated and torn loose from these parts only with difficulty. They are held together by the labrum and epipharynx above, the maxillary sclerites and maxillary processes on the sides, and by the hypopharynx below. From this point the bases of the mandibles and maxillæ diverge cephalad and laterad in a manner which has aptly been compared to the form of the letter "Y." The orientation of these parts was best seen in either a lateral view of the frons, clypeus and other parts removed from the head, or by examining the parts in such a position as to look down on the bases of the setæ in the direction of their distal ends. In such a position this divergence, which takes place immediately cephalad of the hypopharynx and other closely enveloping parts, can be plainly seen. The bases of these setæ (*26*-8, 9) are hollow, funnel-shaped, heavily chitinized, and attached to the other parts by tendons and muscles. One pair of these setæ, from their cephalic position, were recognized as the mandibles, and when dissected out were found to surround the other pair of stylets throughout their entire length, their slightly concave inner surfaces fitting closely against them. This latter, inner pair represents the maxillæ. On dissection they were found to be held firmly between the mandibles on each side and were difficult to separate. The mandibles are thicker than the maxillæ, but not so wide. Their relative shapes can be seen in cross section in *31*-5. As in the cicada, the setæ shortly after leaving the head begin to curve so that the mandibles are above and below the maxillæ instead of laterad of them. This curving was seen in sections distad of the bend of the labium and had begun in the section from which figure 5 was drawn. In this figure the

lumina in each mandible may be seen. These may also be seen running to the tip when the mandibles are viewed extended, as they are generally filled with air, which renders them visible. No indication of lumina could be found in the maxillæ. They, however, by their concave surfaces fitting together, form a canal through which the plant juices are sucked. The tip of a mandible is very slender, sharp, and sickle-shaped, the convex side bearing blunt serrations, the teeth pointing proximad (*26*-7). The tip of a maxilla is of similar shape but with a sharp projection on the convex side some distance from the apex (fig. 6). The apices of these setæ are so transparent that the details of their structure were difficult to discern clearly.

The homologies of the hemipterous mouth have been much discussed in the past, and the opinions held have been various. I have followed the nomenclature used by Meek for *Cicada*, which seems to be in harmony with late investigations along this line. In their place I have compared the parts of the mouth as seen in *Pachypsylla* with the corresponding parts in *Cicada*. I also found in my work that comparison with other homopterous forms was helpful, showing the close relationship of the Psyllidæ to the other families.

The labium of the Aphididæ is quite similar in general structure to that of *Pachypsylla* except in relative length and number of segments and in the fact that it does not possess the bend characteristic of the latter insect.

The mouth parts, exclusive of the labium, are almost identical with, though larger than, those of the Aleurodidæ which I have examined. The same sclerites are present, arranged similarly, though somewhat differently shaped. The labrum is much shorter and smaller proportionately than in this family, and the setæ seem to be relatively shorter. The end of the labium has the same lateral processes, but these are relatively smaller. The Aleurodid labium has a bend similar to that of *Pachypsylla*.

The coccid mouth parts also correspond in many ways. Here the labium is very short and the setæ are retracted into a special pouch when not in use. The parts exclusive of the labium are similar in general structure to the same parts in *Pachypsylla*. Berlese's nomenclature and figures in his work on Italian Coccidæ were very useful to me. According to this,

the clypeus or *ipostoma* (epistoma) corresponds to the frons of *Pachypsylla,* the two terms "ipostoma" and "clypeus" being generally used interchangeably by him. *Cmx* of my figures is the *ipostoma; xyz* is the *rod-shaped apophyse of the clypeus;* the thickened, basal edge of the frons, *z,* is the *transverse bar of the ipostoma;* the opening, *for* (*29*-1), is the *foramen of the ipostoma.* The structure which Meek calls the tentorium is designated by Berlese the *transverse branch of the ipostoma.*

THORAX.

The thorax as described by Riley: "Pronotum moderately short, of equal width, slightly emarginate behind, steeply ascending posteriorly; lateral impressions sculptured and colored as the head; well marked. Dorsulum well developed, thrice as long as the pronotum, and about twice as wide as long; posterior lobe distinctly longer than the anterior; hind margin sinuate each side and truncate at middle; surface finely alutaceous; color, light brownish yellow with a large brown apical spot divided by a yellow median line. Mesonotum convex, wider than head, sculptured as dorsulum, with four vittæ (longitudinal) of brown or greenish-brown color, the outer ones usually wider than the inner ones, all bordered and divided transversely by lines of brighter yellow."

Prothorax.—Viewed from above the thorax is seen to be composed of a number of sclerites, as seen in *27*-3, A and B, which upon closer examination and dissection may be shown to make up the three typical regions of the thorax. In the prothorax there is only one sclerite composing the tergum—the pronotum (*27*-3, A and 31, *pn*). This is collarlike, steeply ascending, as seen in the longitudinal section (fig. 3 B), somewhat wider at the middle than laterad, where an obscure suture divides it from the pleural sclerites. This is shown in plate XXVII, fig. 1, and plate XXXV, fig. 12. The proepisternum and sternum are very closely fused and the suture is scarcely evident. The proepimeron (*27*-1, *em 1*) is a rather wedge-shaped piece, rounded on its ventral end, lying back of the ventral portion of the pronotum and the dorsal portion of the proepisternum. Situated in the pleural membrane beneath the proepimeron is the prothoracic spiracle, *sp.* As seen in *35*-6, the prosternum is only slightly developed, its cephalic edge on each side being produced entad into a slender portion. The prothoracic coxæ are large and occupy, together with the

labium, which is imbedded in a membranous fold between the former, most of the prosternal region, leaving the prosternum to develop mostly on the sides. The "collar," already described as a chitinized process holding the labium to the thorax, may be of the nature of the apophyse as seen in the endoskeleton of the mesothorax.

Mesothorax.—The mesothorax is next in complexity of structure, naturally being larger and more complex than the prothorax, as it bears, besides one pair of legs, the fore wings. The tergum is composed of three sclerites (*34*-2, and *27*-3, A, B). Edwards thus describes the mesotergum of the Psyllidæ: "Mesonotum large, generally suborbicular; a portion of its area in front in the shape of a broadly truncate triangle (the *dorsulum*), separated from the remainder by a distinct suture, and a small crescent-shaped piece projecting from the middle of its hind margin (the *scutellum*), also marked off by a suture."

The dorsulum (*27*-3 A and 1) is in shape an equilateral triangle, truncate at its angles, with the edges of the lateral truncations notched. The posterior margin is not straight, but produced on each side into a small projection midway between the median line and the edge of the sclerite. The anterior third of the dorsulum is covered by the posterior edge of the pronotum (fig. 3 A).

The mesonotum (*27*-3 A and 1, *mm*) is the largest sclerite of the thorax, ovate, convex, and about twice as wide as long, with anterior margin almost straight and posterior margin deeply convex. The sclerite is laterally narrowed to a blunt, notched point, which is best seen in lateral view (fig. 1).

The scutellum (figs. 3 A and B, *scu*, and 1) is, viewed from above, ovate, twice as wide as long, lateral edges rounded, anterior margin slightly concave and posterior convex and hollowed out at the median line. The structure of the pleurum of the mesothorax is exceedingly complicated and the sutures are all indefinite. The structure of the same is shown (partly diagrammatic) in figure 1. The suture between the mesosternum and the sclerite just dorsad could generally be made out. This latter sclerite I take to be the mesoepisternum, *es 2*. The mesoepimeron, *es 2*, is a very irregular, much folded sclerite intimately connected with the inwardly extending endoskeleton (fig. 2, *es 2* and *end*). These pleural sclerites are so folded

and fused one upon the other that practically only the region of each could be indicated roughly in figure 1. The origin of the anterior wing may be seen in figure 1, *bp*. Just cephalad of its base are two fleshy processes—the cephalic, larger and somewhat reniform in shape; the articulatory epidemes, *artep*. Cross sections show the larger epideme to be almost spherical, with a broad, short base or pettiole.

The mesosternum is rectangular, wider than long, anterior margin somewhat convex, with corners rounded. The coxal cavities or acetabula are large, ovate, and are situated on the posterior margin (*35*-11).

When the mesothorax is dissected free from the other segments, and viewed from behind, the endoskeleton is plainly seen. I shall not attempt to give the orientation and detailed description of its different parts, which may be seen in *27*-2 (partly diagrammatic). This internal skeleton is a complex of plates and rods, braced in all directions, and fused with the outer sclerites of the segment. Three different internal projections may be seen, dorsal, lateral, and ventral. The dorsal piece, the phragma, *phrg*, is a symmetrical, transverse plate projecting ventrad. A similar structure in the mesothorax of a stag beetle is figured by Packard (Textbook of Entomology) and called "Diaphragm for the attachment of the tergal muscles of the metasternum." On each side there is a simple projection which seems to correspond to the apodeme, *apod*. The lower projection or apophyse ("medifurca," according to Packard) is seen at *apoph*, and in *35*-11, and is shaped like a letter "Y"; its dorsal edge is hollowed out, this hollow together with a similar one on the lower edge of the phragma above giving passage to the digestive system, etc. (*27*-33, *c*.)

The mesothorax is built for great strength, the sclerites being much fused and the internal structures all large and heavy. Although this segment carries the anterior wings, which are used mainly in flight, I have no evidence that this insect is a very strong flyer; on one occasion a specimen was captured on the top of a high building, but probably it was carried to such a height independent of its own flying powers, by a strong wind blowing at the time.

Metathorax.—This segment is the strongest in structure of the thoracic segments, and the endoskeleton and external sclerites are so strongly fused that the homologies of this region present a great many perplexing problems. I shall proceed to

describe the different parts as I have found them, together with my interpretation as to their homologies. The structure of the notum is not so difficult to determine. Three sclerites are plainly made out (*27*-3 A). The anterior of these is crescent-shaped, and in life is concealed by the scutellum of the mesotergum. The dorsal portion of the second sclerite is a small ovate plate, while the third and posterior sclerite is rather broad, its posterior margin somewhat indented and its lateral margins concave.

The metasternum (*27*-5; *30*-8; *31*-7, *str*) is best developed anteriorally where it is connected with a very light, narrow, median portion between the acetabula, which in turn is connected with and almost seems to be a part of the metafurca, *mf*, of the endoskeleton. Closely connected to the internal pieces of the latter, and separated from the sternum by an obscure suture, is a sclerite whose dorsal end fuses with the other parts. This probably represents the region of the metaepisternum (*31*-7, *es 3*). The portion (*x*) in figure 7 which runs ventrad and entad to join a part of the metafurca has notches on its ventral edge at *x*, and with these notches articulates the end of a complex of sclerites extending down the side and across the ventral surface of the segment (*27*-5 and *31*-8). Much difficulty was found in homologizing these sclerites, authorities differing as to the names of some of the parts. Upon tearing loose this complex carrying the metathoracic leg from its attachment at *x* and *y* (*31*-8) and examining it under a high power of the microscope, its structure could be made out. It is composed of five sclerites. Entad (somewhat caudad and dorsad) is a more or less crescent-shaped sclerite (fig. 8, *str*). This I believe to be a part of the sternum. The next sclerite, *mer*, extad and cephalad, is of a similar shape but bears a blunt projection or tubercle. Authorities differ as to what is the homology of this part. Westwood says: "Beneath, the epimera of the metathorax are singularly produced behind the place of insertion of the hind legs (which are pushed forwards), and terminated by two strong spurs." Edwards states: "Mesosternum produced behind into two large, sharp spines." Riley states: "Metasternal processes cylindrical, hardly narrower toward the tip, which is obtuse, not pointed." I find a similar structure in all the Cicadidæ which I have examined. In "Les Cicadines D'Europe," translated from the German of Fieber by Reiber (1875), in the discussion of the general structure of

the Cicadidæ, under legs, this sclerite is called the "meracanthus" ("A la base des hanches et spécialement aux postérieures, naît, visible chez les Fulgorides et remarquablement développée chez Cicada, une épine subulée, au lobe triangulaire, lancéolée, cornée, qui est encore assez distincte aux hanches intermédiaires, Le Dr. Hagen [Die europ. Cicaden, Stett. ent. zeit. 1886] appelle *trochanter* [Klappe] cet appendice corné qui doit être désigné sons le nom vrai de *Meracanthus*, pl. 10, fig. 9, b, car le trochanter n'a pas d'apendice").

Focusing upward with the high power, the next sclerite, also crescent-shaped, with parallel edges, which is seen to be the next extad, comes into view (fig. 8, *em 3*). It is this sclerite which articulates at *x* and *y* (figs. 7, 8). This I believe to represent the metaepimeron. Cephalad and laterad of these sclerites is a platelike piece, the cephalic end of which bends dorsad and entad, and forms a ring. This structure is seen in figure 8, *cox*. On this ring, the trochanter articulates (also upon the end of the episternum), and since this sclerite is the only one which in any degree approaches the typical cylindrical coxal form, being in this case a sort of ring at its end, I take it to be the coxa. Entad (dorsad) of this, and slightly cephalad, is an accessory sclerite (*35*-8 and 9, *scl*), a rod whose caudal end is flattened out into a plate to which are attached muscles that arise from the inner surface of the meracanthus, or epimeron (which of these two, I am as yet unable to state). The cephalic end is connected to the cephalic edge of the trochanter and serves to pull it towards the body. Its position is shown in figure 8, plate XXXV.

Turning now to the internal structure of the metathorax, which is best seen from the front, when this segment is severed from the others the metafurca (*30*-8; *31*-7; *27*-5, *mf*) are the most prominent features. The two large forks which proceed dorsad and caudad are connected with the lower surface of the tergum. The whole endoskeleton is so closely fused with the sclerites of the metathorax that it cannot always be separated from them. This internal structure is large and heavy, and by bracing all parts makes the segment exceedingly strong and rigid.

The structure of the pleural sclerites in a species of Aleurodid which I examined was also found to be very complex, there being a large number of sclerites homologous to those found in

Pachypsylla, and a careful comparison of the two forms would throw much light on the question.

The metathorax is not so heavily braced as in *Pachypsylla,* but the coxal region is still well developed. A study of the psyllid pupa would probably show much of interest in this connection, as these parts above mentioned are all represented there but somewhat simplified. The folding and fusion of parts in the adult, and the presence of a heavy, braced endoskeleton and the complex articulation of the trochanter of the metathoracic leg, are all specializations to render possible and increase its jumping power.

My studies on the thorax of the Psyllidæ agree with the recent articles by Snodgrass (1909), in which the old theory of Audouin making each tergal segment to be composed of four primitive sclerites is discredited; I have been able to find no more than three sclerites composing the mesoterga and metaterga.

WINGS.

I. VENATION.

The wing venation of the Psyllidæ seems never to have been reduced to any uniform system such as that of Comstock and Needham (1898-'99). I find the venation figured by Mally, Edwards, Slingerland (1896) and others, but the nomenclature is not uniform and is of a special nature. I have attempted to reduce the venation as seen in the insect under discussion to the system of Comstock and Needham, above mentioned. In this study my first conclusions as to the homologies of the veins were arrived at through the study of adult wings alone, but later I have made use of nymphal wings and wings of newly emerged adults.

On March 6 a large number of pupæ of *Pachypsylla celtidisgemma* were procured from their galls on the stems (lateral buds) of the hackberry, some seven or eight being found in each large-sized gall. Their wing pads, after soaking for about a day in dilute formalin, were removed, mounted in dilute glycerine, and studied with special reference to their tracheæ. As soon as I had begun this study I found that my conclusions arrived at earlier were borne out in almost every detail by the number, position, character, etc., of the tracheæ of the nymphal wings, these tracheæ corresponding to the veins of the adult wing.

Venation of Nymphal Wing Pads and Wings of Newly Emerged Adults.

Fore Wing (*26*-3 and *32*-8).—The costa, *C*, rises from a large tracheal trunk from the thorax, proximad of the radius and subcosta (fig. 3). It follows the anterior margin, but drops down at the region of the stigma and fuses with the subcosta.

The subcosta, *Sc*, and radius, *R*, are fused throughout the basal third of the wing, and the free portion of the first-named vein is comparatively short, as it soon fuses with the costa.

The radius is represented by a single trachea, and at its base, where it is fused with the base of the subcosta, it rises from the large tracheal trunk, distad of the origin of the costa (fig. 3).

Media and cubitus, *M*, and *Cu*. The media rises from the main trunk just cephalad of the base of the cubitus and distad of the base of the subcosta (fig. 3). It is two-branched and shows its double structure throughout the distal half of the pad, the two branches being close together and parallel for some distance. The three tracheæ, the subcosta plus radius, the media and the cubitus run parallel throughout the basal third of the wing. In normal position, these three tracheæ are very close together, as in figure 8, but in the diagram (fig. 3) they are represented more widely separated to show their connections with the main tracheal trunk from the thorax. The occurrence and relative positions of these three tracheæ are of the greatest importance in correctly determining the homologies of the adult veins, as the upper of these branched veins, formerly called the "upper branch of the cubitus," arises from a trachea distinct from the true cubital trachea, and therefore cannot be a part of the cubitus, while the trachea representing the subcosta plus the radius fused is distinct from those of media and cubitus, though all four veins appear as a single vein in the basal portion of the adult wing. Both media and cubitus are two-branched, their distal ends bending so as to run parallel with the costa for some distance before fusing with it, forming at some places as many as three parallel or more or less intertwining lines of tracheæ (fig. 3).

The anal fold or "claval suture" (fig. 3, *af*) is present as a distinct trachea which fuses at its distal end with the second branch of the cubitus and the costa near the posterior margin. Only one anal vein (fig. 3, *A*) could be made out, but as this

trachea was torn more or less when the fore wing pad and the hind wing pad, which are grown together at this point, were separated, such evidence in itself is not conclusive. However, from my studies I have every reason to believe that normally only one anal vein is represented. Likewise, the basal connections of the costa of the posterior margin and the trachea of the anal fold to the main trunk from the thorax could not be accurately determined.

For the further study of the development of the venation, a number of *Pachypsylla celtidis-mammæ* which had emerged during the fall of 1908 were thrown into weak formalin immediately after emergence, before the chitinized veins had been laid down (*26*-4; *32*-9, 10 and 11). In one specimen (*26*-4 and *32*-9) the wing was still delicate and transparent, with its edges crumpled and folded, and the veins still practically in their tracheal condition, while in other specimens the wing membranes had hardened, the pattern gained its pigment, though still light, and the veins fully formed but with the tracheæ in some cases visible within them (*32*-10 and 11). In the youngest specimen mentioned above the three parallel tracheæ of the subcosta plus radius, media and cubitus were strictly separate and corresponded in position to those of the nymph of *P. c.-gemma*. The distal ends of the veins, becoming lost in the folds of the margin of the wing, could not be traced. The position and direction of these tracheæ here were more closely like the veins found in the adult than were those of the nymphal wing pads.

These studies aided me much in studying the development of the tracheæ into veins, and the coalescence of two or more of the former into one vein, as seen in the case of the subcosta plus radius, media and cubitus. In some specimens these could be seen to be still single and parallel until they reached the internal trunk (*26*-4 and *32*-9). The radius and subcosta fused (*32*-10) was on the cephalic margin of the compound vein in process of formation, the cubitus (fig. 11) being on the caudal margin.

The vein in the anal fold could still be plainly seen (*26*-4), but its basal connection was not made out. Since there is no thickening of the wing here, as soon as the air leaves this trachea the only suggestion of a vein that is left is the transparent "fold."

Since there is so little chitinization and thickening of the membrane around the tracheæ of the hind wing, these can be studied best in specimens such as the above, where air in the tracheæ renders them visible. This is especially true of the costa, subcosta and vein in the anal fold. The subcosta cannot be made out in the adult hind wing, and has not been figured for it, but shows plainly when filled with air. By placing a piece of black paper under the condenser of the microscope the veins appear a glistening white, and under the low powers are much more easily studied in this manner.

An interesting point I observed in the hind wing was the presence—in one specimen—of what should probably be regarded as a "sport" vein (*26*-2, *sv*). It is connected with the anal vein and also fuses with the costa. Since I have found in one hind wing of two specimens, both male and female, the radius forked, as is the case with the normal cubitus, which branch, though a "sport," probably points back to a former two-branched condition of that vein as seen in the fore wing, this vein above mentioned may show the same condition for the anal wing, and represent the second anal vein. I find under "Psyllidæ" in the "Zoölogical Record" for 1867 the following: "From the occurrence of irregularities in the venation of the wings of this species,[*Anisostropha ficus* Linn.] he [Frauenfeld] takes occasion to remark upon the frequency of such irregularities among the Psyllidæ; the variation is almost always confined to one wing."

Adult Venation.

Fore Wing (*27*-6).—The costa can be easily traced around the entire margin of the wing and is very thick at the basal portion of the anterior edge. All the rest of the veins except the anal arise from a single main trunk, which is the main support for the wing. This trunk is composed of the three tracheæ mentioned above, fused—the subcosta plus radius, media and cubitus. The subcosta and radius are fused as far as the stigma, *s*, where the subcosta runs up toward the costal margin, forms the lower margin of the stigma, and meets the costa somewhat proximad of the apex of the wing. The radius is composed of a single vein, probably representing R 4 + 5. At about the middle of the cell, *I*, a vein leaves the main trunk which divides into two branches, each of these again dividing once. The two upper branches represent M 1 + 2, and M

3 + 4. In one specimen of *Psylla coryli* I found that on one wing the media was single instead of two-branched, but never found such a case in the present species. The two lower branches above mentioned are *Cu 1* and *Cu 2*. Below this is what is called the "claval suture," corresponding to the anal fold (fig. 46, *af*). The region posterior to the anal fold or claval suture is generally called the "clavus," from the corresponding region in heteropterous wings, *cl*. One anal vein is present; this, by a dorsal and cephalic folding over of the distal half of the margin of the clavus, takes the place of the costa at this point (that is, forms the posterior edge of the wing here), the two veins appearing upon first observation to have crossed. This condition was also observed in the nymphal wing pads and in the wings of newly emerged individuals.

Hind Wing (*27-7*).—This is more simple in venation than the fore wing. The costa soon becomes weak and indefinite. The subcosta is not visible except in newly emerged individuals where the tracheæ are filled with air, and the radius is seen as in the fore wing, as a single vein. The media is also a single vein, though in two specimens I found it two-branched in one wing after the fashion of that vein in the fore wing. The cubitus has two short branches. The claval suture and anal vein are practically the same as those in the fore wing, only there is no folding over of the posterior margin of the clavus.

The adult wings as above described are specialized by reduction, the coalescence of veins being outward.

According to Mally's nomenclature, the common base of the media and cubitus which joins the subcosta plus radius is known as the "Petiolus cubite," *Pc;* the media and cubitus before branching are known as the "first cubitus" and the "second cubitus," and their branches the "first, second, third and fourth furcal veins." The presence of a media is not recognized by him.

Edwards calls the media and cubitus the "upper and lower branches of the cubitus," and the "Petiolus cubite" of Mally the "Stalk of the cubitus." He mentions no media.

Woodworth (1906) adheres to a nomenclature somewhat different. According to this, the media and cubitus are called the "independents" which "appear as a twice-forked branch

from the primary," the fact that these veins are distinct, arising from separate tracheæ—as I have shown—not being recognized.

The Psyllidæ are the highest of the group Phytophthires of the Homoptera. These all have simple wing venations, that of the Coccidæ being the simplest. Woodworth says of these: "The venation of the Phytophthires has a nomenclature of its own, not relating it to any other groups, the only investigator who has attempted to homologize the veins being Redtenbacher. This author admits to only two branches as belonging to vein V (corresponding to my independents) [vein *m*] in the Psyllidæ, and sees none at all in the Aphididæ."

II. PATTERN.

Fore Wing.—I quote Riley's original description of the wing markings of this species: "Front wings narrower and, therefore, apparently longer than in *venusta*, very little wider at terminal third than at basal third; costal margin at base but slightly subhyaline, more or less densely covered with small, brownish, scalelike specks, as follows: an oblique and gradually narrowing band (extending from the tip of the pterostigma to near tip of radius), which runs across the wing to the tip of the first furcal, is usually freer from these dots than the rest of the wing, while its edges are usually more crowded with the dots, so as to bring the pale band into greater relief; quite frequently there is an intensified patch of brown about discoidal part of subcostal vein and at all vein furcations; also, the terminal space outside of the pale oblique band is uniformly dark, but with three marginal pale spots (one on each side of the cubital, second marginal and discoidal cells), always more or less evenly speckled; exceptionally, both inside and outside the oblique band, there is a border of variable extent, of a uniform dark brown color, not composed of small dots."

There is great sexual difference in color pattern and in intensity of markings, as seen in figures. The dark border of the light band mentioned in Riley's description is generally very weak in the female, sometimes almost obsolete, except where it crosses the veins, as in figure 6, plate XXXIII. In general, the wing of the male is darker and more heavily marked than that of the female. Also, the spring forms of both sexes are said to be darker than those that emerge in the fall and hibernate over winter.[2]

2. Insect Life, vol. V, p. 227.

In the males there is generally a large dark spot between *Cu 1* and *Cu 2*, and on and below the radius proximad of its fusion with the subcosta, this spot tending to spread across cell I. These spots, proximad from the stigma, tend in the female to be reduced to dusky portions only a little darker than the surrounding parts, the former being almost indistinguishable and the latter confined to a border to the vein. The three marginal spots mentioned by Riley are generally more distinct in the male. There is a great deal of individual variation in the wing markings as to the number and arrangement of the small spots composing the pattern, no two individuals showing precisely the same combinations. Figures 1 and 5, plate XXXIII, show how this pattern is produced, and incidentally the difference in shape of the apices of the male and female wings. Figure 4, plate XXXIII, is another view of the pattern at the branching of the median veins, more highly magnified than the two preceding.

The upper surface of the wing is entirely covered with disk-like cuticular outgrowths about 0.005 mm. in diameter, best seen in cross section through the wing (*30*-9, *a* and *b*). These are more or less circular in outline though often very irregular. Some of these, *b*, are filled with dark brown pigment, the same diffusing slightly into the surrounding cuticula. These pigmented disks are arranged in groups of 2, 3, 4, 5, 6, 7, 8, and so on, to form polygons and other figures. These groups form the "spots" which make up the pattern, and are either distinct or banked up together to form a dark spot or band, in which case the polygonal structure is not so apparent. The following elements make up the pattern: (1) The individual pigmented cuticular processes, which I shall designate as "disks"; (2) polygonal and other combinations of these disks—"groups"; (3) arrangements of these groups making up the large and small spots, bands, etc.—"markings."

There are a great many different forms of groups produced by these disks, the principal types of which are seen on page 146. Polygonal groups predominate, though chainlike, broken, and irregular forms are also found. Groups of "two's" and "three's" arranged lengthwise with the wing are found predominating in the basal cells, while more complex polygonal figures are the rule in the distal regions of the wing. Groups consisting of only one disk were not found.

Any difference between the composition of the groups or the

frequency of certain group types in the male and the female was not found. The polygonal groups are oftener without the central disk dark than with. When this was not pigmented, the space was still clouded the same as the cuticula surrounding the pigmented disks.

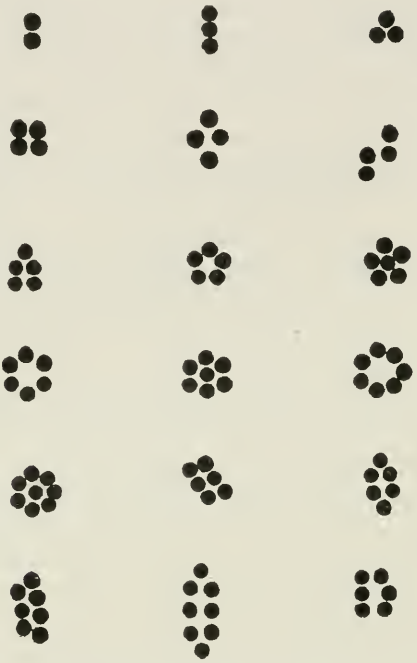

FIG. 61.—Diagram showing principal forms of groups found in the pattern.

The disks were found to be smaller proximad of the base of the wing and near the veins and the anal fold, and consequently the groups there were either of uniformly small disks or of part normal and part small-sized disks. There were no groups on the stigma; here the disks became reduced to mere low, conical projections. The anal fold was smooth and transparent, with clear-cut edges.

Cross section (*30*-9, *c*) shows on the lower side of the wing, opposite each disk, a small, blunt outgrowth, generally unpigmented.

Hind Wing.—Here the disk structure of the membrane is barely visible under favorable conditions of illumination of the microscope. Only those disks on the clavus are pigmented.

The number of groups averages thirty to thirty-five. They tend to be irregular and not polygonal. Groups of "four's" are perhaps the most common, being generally found singly, though sometimes two or three groups are associated together to form a figure, generally a chain.

III. STRUCTURE.

Fore Wing.—Of the sixty wings that I examined, the fore wings averaged 2.94 mm. long by 1.19 mm. at greatest width in the male, and 3.27 mm. by 1.37 mm. in the female. Variations in outline of the wings and in the shape of the cells were very slight. There was, however, variation noticed in the length and breadth of the wing between rights and lefts in both sexes.

In the membrane at the base of the fore wings are found two small sclerites, called by Audouin "articulatory epidemes," already mentioned (*27*-1, *artep*). The cephalic of these is seen in cross section to be more or less spherical in outline.

On each side of the wing veins is a row of rather stiff, curved hairs in circular pits, seen in *33*-1 and 5. On the anterior portion of the costa there are three rows of hairs, the anterior of which is separated from the others by a central, dorsally projecting ridge of the costa. From a point near the proximal edge of the light band, already referred to under "pattern," these hairs are found in a single row until the place is reached where the anal vein and the posterior costa seem to cross. From here on the costa bears no hairs, but in their place a row of very minute, sharp teeth on its outer edge. These teeth are also found on the edge of the anterior costa below the smooth-edged cuticular margin of the wing; they are somewhat larger here, but become obsolete a little before the apex of the wing is reached.

Upper and lower surfaces of the wing are essentially the same, as regards number and position of hairs. The structure of the membrane has already been treated. It is submembranaceous in texture.

Hind Wing.—The hind wing averages 2.5 mm. long by 0.97 mm. wide. The apical portion is wider than the basal and is well rounded. The anterior margin is fairly straight, though somewhat undulating in outline. No hairs are found on the veins of the hind wing except two or three on the fused portion of the subcosta, radius, media and cubitus, and on the basal

portion of the anterior costa, where fifteen or more—the number being variable—long, stiff hairs project cephalad, curving upward (*33*-8). The hind wings are very weak and delicate, and these hairs are of use in coördinating the movements of the hind wing with those of the fore wing, resembling somewhat the "hamulus" of the Hymenoptera.

The anterior margin of the costa is only slightly roughened —covered with low, knob-like processes, distad of the hairs— the basal two-thirds of its length, but from here on as far as the beginning of the clavus these knobs become lengthened out into spine-like scales pointing distad. The margin of the clavus is comparatively smooth except where roughened at the humeral angle.

The membranes of this wing are transparent and thin, and were often separated from each other to form a sac, when boiled too long in caustic potash. This is in harmony with the studies of Weismann, Künkel d'Herculais, Dewitz, Van Rees and Pratt, which established the fact that insect wings are of hypodermal origin, being evaginations of the integument, and the separation of these membranes through the action of caustic potash shows plainly that the wing membrane is made up of two laminæ, an upper and a lower, which are fused to one another between the veins. The veins, except the costa, are almost without chitinization, and the subcosta could be made out only when it was filled with air as in newly emerged specimens.

The fore wing is quite flat, except the clavus, which is bent somewhat ventrad, and that portion of the clavus between the anal vein and the costa is bent quite sharply ventrad, so that it is almost horizontal in position when the wings are folded along the side of the body. When the insect is at rest and the wings are in this position the anal angles of the fore wings fit up closely against the edges of the scutellum of the mesothorax, and their edges are contiguous from the distal end of the clavus to the tip of the wing. Through the gap between the claval portions of the wings can be seen the posterior margins of the hind wings, which are contiguous throughout the claval region, their anal angles fitting against the small oval sclerite of the metathorax (the second tergal sclerite).

LEGS.

The prothoracic and mesothoracic legs are essentially the same in structure, while the metathoracic leg is greatly specialized. The coxæ of the former are not free and movable, as in many insects, but immovably fixed to the thorax, and, according to Witlaczil, coalescing with it. They are greatly produced laterally, this portion being flattened and longer in the mesocoxa than in the procoxa.

The trochanters are short, cylindrical sclerites, somewhat constricted proximally. All three pairs are similar.

The two anterior pairs of femora are swollen, the outlines of their dorsal surfaces somewhat convex, and the cuticula of ventral surfaces much roughened. The femora of the prothoracic legs are somewhat longer than those of the mesothoracic pair. The distal ends are on their ventral faces deeply gouged out, into which groove, bounded by strong lateral edges, the tibiæ fit when the leg is flexed. The femora of the metathoracic legs are similar in structure to those of the other pairs, but longer and relatively more slender. There was very little variation of this part, as may be seen by the following table of measurements:

AVERAGE LENGTH.			
Male.		Female.	
Right.	Left.	Right.	Left.
0.656 mm.	0.654 mm.	0.686 mm.	0.691 mm.

The articulation between femur and trochanter of mesothoracic leg is shown in figure 78, page 150. This is similar in the other pairs.

The structure of the tibiæ is of great interest. The tibiæ of the prothoracic and mesothoracic legs are about as long as the femora, but those of the metathoracic legs are slightly longer than the femora. The distal ends of the first and second pairs of tibiæ bear a fringe of long, sharp spines which point distad, those of the prothoracic pair being slightly the weaker. The distal ends of the metatibiæ are swollen and bear nine short, thick, blunt, black spines (figs 73, 74 and 75). These spines are a part of the scheme of specialization for jumping, preventing the foot from slipping in the same way as do the spines on the grasshopper's tibiæ.

The tarsi are two-segmented. In the first two pairs of legs the second segment is larger, but the first is the larger in the metathoracic pair. In all three pairs the segments are much

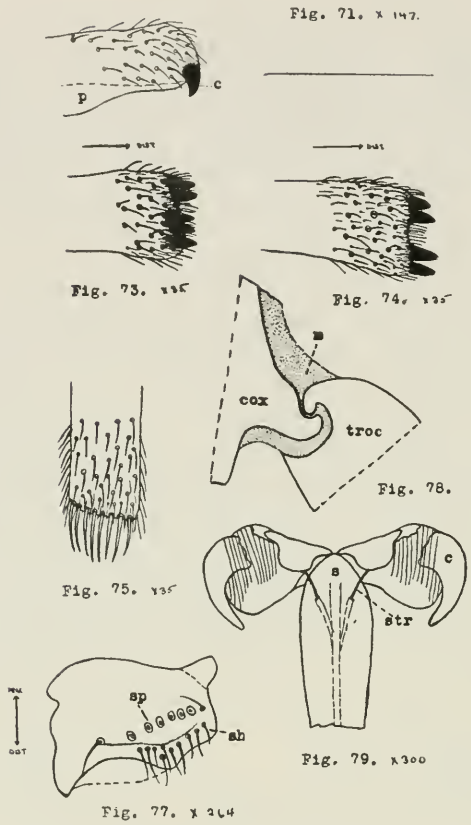

FIG. 72.—First metatarsal segment. *c*, claw; *p*, pad.

FIGS. 73 and 74.—End of metatibia showing spines.

FIG. 75.—End of mesotibia.

FIG. 77.—Metatrochanter. *sh*, sensory hairs; *sp*, sensory pits.

FIG. 78.—Articulation between coxa and trochanter mesothoracic leg. *cox*, coxa; *troc*, trochanter; *m*, membrane.

FIG. 79.—Prothoracic foot. *c*, claw; *s*, *str*, tendons moving claws.

constricted proximally. The first segment articulates with the tibia by a joint much like that between femur and trochanter. On the ventral surface of the first tarsal segment of the metathoracic leg is a soft, membranous pad, projecting distad between the two stout, laterally placed claws (fig. 72). This pad is best developed in the metathoracic tarsi and these claws are found only here.

The second segment bears the claws, which are similar in all three pairs of legs. These are short, heavy, and rather blunt,

with several small sclerites at their bases embedded in the membrane. These are illustrated in figure 79, which shows the tendons controlling their movement, and the two-lobed empodium, one lobe being under each claw. This empodium is functional, as in many insects, and is used in holding the insect to a smooth surface, as it can cling readily to a glass surface.

Femora, tibiæ and tarsi of all three pairs of legs are covered with hairs, many of which are probably tactile. Both coxæ and trochanters (except of metathoracic legs) bear hairs, the latter with one or two hairs on their distal ends longer than the segments themselves. On the trochanters is a row of oval sensory pits (fig. 77, *sp*).

ABDOMEN.

The relative shapes of the abdomen in the sexes can be seen in *35*-13 and 14 (figure inverted), also in *34*-4. The abdomen of the female is larger than that of the male and seems much longer in proportion, as the ninth segment of the male bearing the genitalia is generally carried bent dorsad and cephalad so that the supra-anal plate fits up tightly against the seventh segment, thus making the abdomen appear quite short. In both sexes it is slightly compressed laterally. According to Edwards, there are visible five segments above and six below, not counting the genital segment.

The first two segments are smaller than those caudad. "The first abdominal somite of both sexes is added to the metathorax to enlarge the springing-gear; the second abdominal somite forms a short stalk for the abdomen. . . ."—(Macloskie.)

According to Witlaczil, in the male the supra-anal plate represents the tenth somite, the ninth is not represented above, and below forms the subgenital plate; the eighth is scarcely at all developed above; in the female, the supra-anal and subgenital plates or valves represent the tenth segment.

In the pleural membrane are found seven spiracles, each surrounded by a wide, chitinized ring. The cuticula of the abdomen is punctate, not so pubescent as that of the thorax, and the membrane between the chitinized plates of each segment is covered with great numbers of minute *sensillia styloconica*. On the posterior edge of each segment is a row of

sensory hairs, in prominent pits, much more evident, however, in the male than in the female.

GENITALIA.

MALE GENITALIA.—The genital segment of the male of *Pachypsylla celtidis-mammæ* is described by Riley as follows: "Male genital segment a little longer than the preceding ventral segment, brown, shining; plate as high as the length of the segment, lateral lobe barely indicated, anterior margin straight, posterior margin very slightly oblique, *i. e.*, the plate gradually increases in width towards the tip, which is truncate and not arctuate, as in the preceding species. Forceps as in *venusta* [two-thirds as high as plate, front margin straight, hind margin slightly sinuate at basal half, tip rounded, outer face smooth and very shining]."

The genital segment of the male consists of the following parts: Supra-anal plate or "genital plate," subgenital plate, forceps or "posterior processes," and copulatory organ or "ædeagus."

The supra-anal plate is a conspicuous fleshy process attached to the anterior edge of the subgenital plate. It is generally carried at about right angles to this plate, and is shown in *35*-10 as drawn forward out of normal position. It averages about 0.48 mm. in length (measured on cephalic surface) and its greatest width is 0.19 mm. Looking cephalad at this plate it is seen to taper at top and bottom, and to be convex with rather wide flaps on its lateral edges (*30*-6, *sppfl*). At its distal end these flaps recede to the edge, where the organ ceases to be an open trough, and becomes a short, rounded, truncate, cone-shaped structure (*30*-6 and 7, *x*), connected by its cephalic wall to the basal wall of the trough below. This structure ends in a short, flaring, membranous ring (figs. 6 and 7, *a*), which is the external opening of the anus. The concave face of the plate is lined with a delicate, folded membrane, between which and the cephalic wall is situated a tube, the rectum. Almost the entire surface of the plate carries numerous long, stiff hairs.

The lower extremity of the supra-anal plate consists of a chitinized ring which expands into a rather broad, two-lobed plate, *lp*, on each side. These plates drop ventrad at their inner edges much after the fashion of a funnel, and form the base of the copulatory organ.

Extending ventrad, with its dorsal edges articulating with the lower side of each of the above-mentioned lobed plates, is a chitinized band or loop (figs. 6 and 7, *l*) extending downward almost to touch the inner surface of the subgenital plate. Between the arms of this loop the proximal portion of the copulatory organ swing, almost entirely concealed within the subgenital plate when the genital segment is telescoped into the next segment cephalad and the supra-anal plate is forced caudad. At emergence, however, the genital organs are extended and not telescoped, and at time of copulation the copulatory organ is protruded from the cavity of the subgenital plate.

Extending ventrad from the lateral plates at the base of the supra-anal plate is the chitinized couplatory organ or extremity of and sheath for the penis—"the ædeagus" of some writers. This organ (figs. 6 and 7, *co*, and *35*-7), soon after it leaves the base of the supra-anal plate, forms a sharp bend, reversing its direction to dorsad. After reaching a position about opposite the middle of the supra-anal plate there occurs a conspicuous swelling, and beyond that a joint or geniculation (*30*-6, *g*). The proximal portion of the second segment of the organ is also swollen. This segment in normal position drops ventrad. The distal end bends caudad and is swollen greatly, becoming club-shaped (fig. 6, *c*), convex cephalad, and concave caudad, this segment having a vertical orientation. The convex, cephalic face of the club is gouged out to form a deep longitudinal groove running from base to tip.

The proximal portion of the first segment of the copulatory organ is not tubular, but slitted on its convex surface, and through this slit the penis enters the sheath, *p*. The concave surface of this portion is coarsely notched or corrugated transversely for some distance beyond the bend. The remainder of the organ is tubular, the canal running through the inner half of the sheath—that is, through the cephalic half of the first segment and through the caudal half of the second segment. This canal runs into the center of the club, makes a sharp turn, and, proceeding back upon itself, curves to the convex side of the club, where it issues at the base of the club in the bottom of the groove above mentioned.

The copulatory organ is more strongly chitinized at its distal end than it is in the curved portion of the proximal segment, and along its outer surface, than on its inner. The first segment measures (from base to geniculation, the distance along

curved side being much greater) 0.31 mm., the distal segment 0.38 mm., and the club 0.12 mm.

The subgenital plate has already been mentioned in the quotation from Riley. Its measurements are as follows: Depth, 0.37 mm.; length, 0.40 mm.; greatest width, 0.26 mm.

Situated at the posterior end of the subgenital plate are the forceps (fig. 10, *f*, and *35*-15). These two pieces are somewhat swollen at their bases, seem to be articulated one against the other, and are connected to the subgenital plate by means of a long, thin, tendonous strip, which reaches ventrad to the inner surface of the plate, where it is fastened. The forceps are about 0.29 mm. in length, spread at widest 0.29 mm., and project above the subgenital plate 0.20 mm.

Female Genitalia.—The genital segment and ovipositor of the female are of great morphological interest. The genital plates have been described by Riley as follows: "Female genital segment a little shorter than the three preceding ventral segments together; . . . upper plate a little longer than the lower one, gradually tapering toward the tip, which is straight; . . . lower plate also simple." This is in substance all that I have found in the literature to which I have had access concerning the female genitalia of this family. The genital valves or plates, being of taxonomic value, have generally been included in descriptions of species, but the ovipositor remains unmentioned, except in a few cases where it is spoken of as "ending in an acute point" (Edwards). Westwood (1839) mentions it as a "pleurivalve conical ovipositor." I have been unable to find anywhere a treatment of its structure.

I shall first treat of the two plates mentioned above, and then consider the structure of the ovipositor proper.

Of these plates, the supra-anal is of the greater interest. It is wedge-shaped, with its apex blunt and its proximal end three-sided. It averages in length 0.98 mm. and in width 0.42 mm. Its shape is well shown in *35*-4, where the ovate openings at its basal angles can be seen. These latter may be of use in attaching the plate to the abdomen. The plate is somewhat convex but not so much so as the subgenital plate. It bears on its upper surface sensory hairs, probably tactile, and is quite heavily chitinized except for a large oval space, *y*, about 0.26 mm. long surrounding the anal opening, where the plate is

almost transparent. Along the median line in this space is a slit, into the cephalic end of which the anus opens; this could be seen in a longitudinal-vertical section, where the rectum was found to run just under the dorsal surface of the posterior end of the abdomen and end at the cephalic end of this slit. About midway between this slit and the edges of the clear space are situated the curiously ornamental openings of the circumanal wax glands, outside of which are rather broken and irregular rows of short, heavy, curved, sensory hairs in pits. The dorsal aspect of this region of the plate is represented in *31*-4. This encircling band of wax glands is double; their openings are ovate to rectangular, with borders measuring 0.015 mm. in width, and are seen in the greatly magnified portion shown in *26*-5 B. Longitudinal-vertical sections showed the glands themselves. These are of large size, flask-shaped, with long necks, and are closely packed in a double row under the dorsal openings. They are illustrated in section in figure 5 A, *wg*. Their nuclei, *n*, could in most cases be made out quite plainly. These glands are of hypodermal origin, and are homologous to the circumgenital glands or spinnerets found in the Coccidæ. They are functional in the nymphal stages of most Psyllidæ, and in those forming galls the wax enters into the composition of the gall, making an impervious lining for the cavity, while it is found as a stringy, exuvial covering to some of the nongall-formers. These glands are functional in the nymph of *Pachypsylla*, but I have no evidence that they are so in the adult.

The subgenital plate is much broader and more concave than the supra-anal plate, though not so long as the latter. Its shape when flattened out is shown in *27*-8. The anterior margin is almost straight, except laterad, where it turns caudad and joins the lateral margin, forming an acute angle. The apex is blunt, as in the supra-anal plate. The approximate measurements of the plate are: Width at base, 0.73 mm.; median length, 0.63 mm.; length of lateral margin, 0.67 mm. The plate is covered with rather stiff hairs, probably tactile, more numerous at the posterior end and wanting at the anterior end; it is almost as heavily chitinized as the supra-anal plate.

Ovipositor.—The insects of the suborder Homoptera possess a well-developed ovipositor. This is well preserved and of quite complicated structure in the family Psyllidæ.

The typical structure of an ovipositor is described in the following quotation from Packard: "Morphologically, the ovipositor is composed of three pairs of unjointed styles (*rhabdites* of Lacaze-Duthiers, *gonapophyses* of Huxley), which are closely appressed to or sheathed within each other, the eggs passing out from the end of the oviduct, which lies, as Dewitz states, between the two styles of the lowest or innermost pair and under the cross-bars or at the base of the stylets mentioned; the styles or blades spreading to allow of the passage of the egg."

The structure of this organ I find to be second in interest only to the mouth parts. It is more complicated in structure than those parts in the cicada, but the homologies between the two can be worked out in part, as will be seen later. It is very similar in most points to the ovipositor in the Aleurodidæ.

Lack of material has confined my work to postembryonic studies. There has been much investigation on the segmental origin of the ovipositor parts, the researches of Wheeler and Heymons being of chief importance. Wheeler (1892), who studied orthopteran embryology, holds for the "direct continuity of the embryonic appendages with the gonapophyses," while Heymons (1899), from studies in Heteroptera and Homoptera, considers these gonapophyses as hypodermal outgrowths. However, it is not my purpose to discuss these questions, but to treat of the anatomy and homologies of the parts.

A specimen of *Pachypsylla* female, mounted in balsam after having been thoroughly boiled in caustic potash and cleared, showed, when viewed from the side, the relative position of the ovipositor as regards supra-anal and subgenital plates, and the posterior abdominal segments (*30*-4). The ovipositor is seen to be an elongate organ with dorsal and ventral outlines about parallel. It measures in length about 0.82 mm., in greatest width about 0.19 mm., and in thickness less than half that of width. The caudal extremity is acutely pointed, this portion bending dorsad, then caudad, with its apex extending caudad even with the tip of the subgenital plate, while the supra-anal plate extends caudad from this apex 0.11 mm. in the specimen described. The proximal or cephalic end of the ovipositor is composed of several sclerites of irregular form, to be described later, the ends of which project 0.16 mm. beyond a line joining the bases of the enclosing external plates to a

position about opposite and above the last spiracle, well into the dorsal portion of the last abdominal segment. Its position relative to the two plates is shown in figure 1 B, plate XXVI.

Seven longitudinal rods or valves are to be found running throughout the organ. Six of these are paired, two pairs forming the lateral edges of the ventral face of the organ, and a third pair lateral and well towards the dorsal face; the seventh and unpaired rod is dorsal and median.

Each upper and each lower valve of the two ventral pairs are very closely connected, being held together throughout their entire length by means of a tongue on the upper fitting into a groove in the lower, which may be seen in the cross section in *26*-1 A, *tg*. The tips of these valves are very sharp and finely pointed, and come together at their tips, where they are enclosed in a sheath. The cephalic ends of each ventral and inner stylet is connected with a more or less crescent-shaped sclerite (*26*-1, *blv*). The cephalic end of each ventral and outer stylet connects with a sclerite (fig. 1, *buv*) which runs dorsad and caudad. When this reaches about the dorsal face of the ovipositor it turns caudad and becomes a thin rod, *lr*, and at about the middle of the ovipositor becomes compressed laterally to form a wide, thin plate, which gradually loses its chitinization, and is lost in the fleshy tongues on each side of the ovipositor sheath (figs. 1, 2 and 3, *stp*).

Situated medially and a little dorsad of the above-mentioned rods is a rather thick, cylindrical rod bent at its cephalic end slightly dorsad, then ventrad (fig. 1, *mr*). This rod does not project quite as far cephalad as the stylets below. It is greatly swollen at its caudal extremity, with a square end, and its ventral portion is continued into a slender process, in shape much like a human femur, *procv*. This last-named process works against a ventrad-projecting outgrowth of the sheath surrounding the stylet tips, which serves to close the oviduct (fig. 1, *v*). Lying above this slender sclerite are two pairs of chitinized sclerites (figs. 1 2 and 3, *sc 1* and *sc 2*), which are connected with and probably serve to bring about lateral adjustment of the lateral tongues above mentioned. Viewed laterally, these sclerites appear as one pair (fig. 1), but when viewed from above, and pressure was applied to the dissection so as to spread the sides apart, they were seen as two distinct pairs of sclerites. Viewed in this manner, the sclerites

of the cephalic pair, *sc 1*, are pointed, with convex inner surfaces. Their tips have a connection with the lateral plates (figs. 1, 2 and 3, *pl*), the latter probably serving to spread these sclerites apart. The caudal pair, *sc 2*, reach almost to the base of the sheath surrounding the stylet tips, are rectangular in shape, with rounded ends, and with their inner surfaces corrugated, the corrugations corresponding to the striations on the surfaces of the lateral tongues of the ovipositor.

The sheath already mentioned (figs. 1, 2 and 3, *sh*) is slitted on its dorsal surface from near its cephalic edge to the apex of the ovipositor, to allow of the spreading of the stylets and the passage of the egg during oviposition. The cephalic portion of its dorsal face carries the small, valve-like, ventrad-projecting process (fig. 1, *v*).

Fig. 1, pl. *26*, shows a cross section about midway through the organ. In this the fleshy structures that were destroyed in boiling in caustic potash can be made out. The grooved and toothed valves, *uv* and *lv*, are seen fitted together, and the chitinized portion, *x*, which is grooved and forms the sides of the oviduct. Above the oviduct, and forming its roof, is the structure, *y*, whose ventral surface is covered with minute, soft, hair-like outgrowths, and whose dorsal portion is chitinized. The part marked *z* probably represents the lateral plates, *lpt*, of *30*-1, 2 and 3. The duct of the cement (?) gland is seen at *cmgd* in this figure and appears in all sections cephalad of this, and in those caudad up to the point where it turns ventrad and enters the oviduct. The entire course of this duct was best seen in longitudinal-vertical sections, but could be traced well in longitudinal-horizontal sections, where its union with the oviduct was plainly seen, and in the next succeeding sections ventrad the oviduct was laid bare. The cement (?) gland itself, a small sac, was found somewhat cephalad of the base of the ovipositor in most of my dissections. Figure 6, plate XXXI, is of a cross section near the base of the ovipositor sheath. Here the shape of the supra-anal and subgenital plates can be seen, also the position of the oviduct. The lateral tongues or sting-palpi are also represented.

I have pointed out the structure of these parts and shall now give my theories as to the homologies. The typical struc-

ture of an ovipositor as being composed of several pairs of stylets has already been mentioned.

To homologize the structure of the ovipositor of *Pachypsylla* with the structure of the typical ovipositor is more difficult than the comparison of it with that as seen in the different families of the Homoptera. I find that it is more specialized than a typical ovipositor such as found in the Orthoptera, though it is possible to show the homologies; but since it resembles more closely that found among the Hymenoptera—where it is specialized to form a sting—these homologies can be traced through the latter. Taking the sting of the honeybee as a type of the hymenopterous ovipositor, since this has been so carefully worked out by Cheshire and others, it can be seen that the lower valves of *Pachypsylla* (*30*-1 and 3, *lv*) correspond to the lower and outer pair of *darts* in the honeybee. The upper valves of *Pachypsylla* correspond to the inner pair in the bee, where they are fused into one piece to form the *sheath*. It should be noted here that the *sheath* does not correspond to that part of the ovipositor of *Pachypsylla* which I have designated by that name. In the honeybee there are two fleshy processes, one on each side of the sting, which are thought to represent the upper pair of stylets and are called the "sting-palpi" or "feelers." These are evidently the same as the lateral tongues found in *Pachypsylla*.

The homologies up to this point are comparatively clear, but as to the remainder of the parts I can only theorize, as their structure is complicated and there are present more pieces than in the typical organ. The lateral tongues evidently are the "sting-palpi" and together with the *lateral rods* and *lateral plates* form the upper pair of stylets; but this explanation does not account for the *median rod* with its processes and appendages. There may be three possible explanations for these structures:

1. This *median rod* might be regarded as a fusion of the dorsal pair of stylets, and the *rods* and *lateral plates* only as tendons causing the spreading of the *sc 1* and *sc 2* and consequently the *sting-palpi*.

2. The *rods* and *lateral plates* might be considered as composing the dorsal pair of stylets and the *median rod* as an accessory structure which, moving backward and forward, would spread and close the *sting-palpi*, for these latter are

evidently in as intimate a relation to the *median rod* as the *lateral rods*. Hence, there is possible a third theory:

3. According to Lacaze-Duthier's view, there are "two pieces forming the outer pair of rhabdites" (after Packard), as seen in the figure illustrating his conception of the ideal ovipositor. In *Pachypsylla, one* of these "pieces" might be the *rod* and the *lateral plate* which connects basally with the lever supporting the base of the upper valve, *buv*, and distally with the tongues or *sting-palpi*. The *median rod*, then, might represent the second of the "pieces," its two parts fused into one. Thus *rods* and *lateral plates*, together with the *sting-palpi*, would form one portion of the upper pair of valves while the *median rods* represent the other paired portion, fused. The sheath may also belong to the second piece of the upper valves, as do the two pairs of small sclerites, *sc 1* and *sc 2* (*30*-2). The levers supporting the bases of the lower valves, *blv*, find their homologues in similar structures in the honeybee, termed there simply "levers," which are the point of attachment of muscles moving the sting. They have a similar function here, serving to spread the styles.

The ovipositor of the cicada has been described and figured by Marlatt (1895). A rather superficial study of this form from my own dissections has rendered the following facts and hypotheses as to the homologies between this form and *Pachypsylla:* There are found two pairs of blades, the dorsal pair grown together, and the two pairs sliding on one another by means of tongues and grooves much as I have shown to be the case with *Pachypsylla*. The tips of the ventral pair of blades are serrated for cutting purposes. These two pairs of blades evidently correspond to the upper and lower valves or styles of *Pachypsylla*, though in the latter there is no need for their tips to be modified for cutting, as the eggs are not deposited within plant tissue. In *Cicada* there is a very large sheath surrounding the entire ovipositor, except for a slit beneath, which probably corresponds to the supra-anal plate. Marlatt says, "The ovipositor is protected and covered when at rest by two valves, which form a sort of sheath or scabbard." These second valves mentioned by Marlatt, which are dorsad of the blades, proximad are broad, and made up of chitinized and more or less membranous portions, and distad are composed of two distinct and distally separable scabbards

covering the tips of the blades dorsally and laterally, and open entad and ventrad. The basal portion is evidently a complex made up of parts corresponding perhaps to the *median rod, lateral rods* and *lateral plates*, with their processes, appendages, etc., of *Pachypsylla*, while the two scabbards may be homologous to the *sheath*. The *sting-palpi* are not represented in *Cicada*.

The ovipositor of one species of Aleurodidæ which I have examined showed features most similar to those of *Pachypsylla* of any other insect, the parts being much more easily compared with those of this insect. The upper and lower pairs of converging blades or styles were found, together with a sheath enclosing their apices, while their bases bore irregular supports as in *Pachypsylla*. *Sting-palpi* and *sc 1* and *sc 2* were also present.

GENERAL SUMMARY.

1. The head is made up of the typical sclerites.

2. The mouth parts conform in general to those of other homopterous forms, such as those of the Cicadidæ, Aphididæ, Aleurodidæ, and most closely to those of the Aleurodidæ, differing most from those of the Coccidæ.

3. The mesoterga and metaterga show three sclerites only. The pleural sclerites are much folded, with their sutures almost obsolete. The internal skeleton of mesothorax and metathorax is large and heavy, making the segments very rigid.

4. The metathoracic legs are greatly specialized for jumping, the tibiæ being provided with heavy spines on their distal ends, and the coxa, epimeron, meracanthus, a part of the sternum, and an accessory sclerite compose a single complex of sclerites which encases powerful jumping muscles.

5. A study of the tracheation of nymphal wing pads and wings of recently emerged adults has shown that there are present in the adult wing the following veins: one costa; one subcosta; one radius; one two-branched media; one two-branched cubitus; one anal vein; and a vein occupying the anal fold, seen only in nymphal wings, being represented only as a fold in the adult wing. Previous writers have not indicated the media and cubitus as separate veins, but I have shown them to be represented by separate parallel tracheæ in the wing pads. The subcosta of the hind wing, previously unfigured, was found in recently emerged specimens. A sport vein, pos-

sibly representing the second anal vein, was found in one specimen.

6. The color pattern was found to consist of polygonal or irregular groups of pigmented, disklike outgrowths of the cuticula. The manner of producing the pattern is various.

7. The male genitalia were found to consist of supra-anal plate, subgenital plate, couplatory organ and forceps.

8. The female genitalia consist of supra-anal plate (ornamented with a double row of wax glands, flask-shaped in longitudinal section), subgenital plate and ovipositor. The ovipositor was found to be homologous in many points to a hymenopterous ovipositor as seen in the honeybee (a sting). Comparison with other homopterous forms showed it to be homologous in most points with that of the cicada, but almost identical to that of the Aleurodidæ, showing, with the buccal appendages, the close structural relationship of the Psyllidæ to that family.

TECHNIQUE.

My studies have been based upon dissections and serial sections.

Dissections were made in three ways: (1) A dissecting stand fitted with an 0.8-inch lens was used in some cases; (2) some of my work was done under a compound microscope (one-inch eye-piece and one-inch objective) on the lower end of whose draw-tube was placed a three-inch objective, thus producing an erect image. This combination was useful but its disadvantage was that the eye was too far from the specimen being dissected on the microscope stage; (3) the greater part of my dissecting, however, was done under a "Pfeiffer's Erect-vision Dissecting Microscope" using objectives three inch, one inch and two-thirds inch. This was found to be the most convenient, especially in the more delicate dissections, such as of mouth parts and genitalia. By the use of very fine, sharp-pointed needles, these minute organs could be torn apart with ease.

Most of my material was boiled for a short time in caustic potash, and then treated with alcohol and xylol previous to dissections, no fresh specimens being available at the time when this work was done. Xylol was of great use in clearing the parts, but at the same time it rendered them brittle and easily broken.

Dissections were made under water, alcohol, xylol and glyc-

erine. Xylol was a very clear medium, having the advantage that uncleared specimens could be dissected in it, soon becoming clear, but it evaporated very quickly, and, lacking viscosity, allowed too much movement of the parts being dissected. Glycerine was found to possess the necessary viscosity and was the most satisfactory medium in most cases.

The nymphal wing pads were removed with fine scissors, holding the nymph the while between the finger-tips; the pads were mounted in dilute glycerine after being kept in formalin for about twenty-four hours.

Serial sections were made through the mouth parts and genitalia, and cross, longitudinal-horizontal and longitudinal-vertical sections through the entire insect.

Killing and Fixing.—Live insects were killed by plunging into a boiling saturated solution of corrosive sublimate containing about one per cent of acetic acid, and after being punctured with a piece of glass drawn out into a fine point were left in the solution to fix for twenty-four hours.

Dehydrating and Clearing.—The insects were placed in small vials with ends covered with cheesecloth, and run through alcohols of percentages 70, 85 and 95, twenty-four hours in each. They were removed to absolute alcohol for about twelve hours and then run into xylol for about twelve hours.

Infiltration and Embedding.—Leaving the specimens still in the vials they were infiltrated in a paraffin oven with paraffin of melting-point 50-55° C. for forty-eight hours. They were then embedded in paraffin in small paper dishes, being oriented properly as the paraffin hardened when the dish was floated on cold water.

Sections.—Serial sections 10-20 microns thick were cut on a sliding microtome. The ribbons were floated onto Mayer's albumen fixative on a clean slide, the excess of fixative drained off with filter paper, and the slide dried on top of the paraffin oven for twelve or more hours. The slide was then left for ten to fifteen minutes in xylol to remove the paraffin, when it was run through the following grades of alcohol, five to ten minutes in each: 95 per cent, 85 per cent, 70 per cent, 50 per cent, 35 per cent, 25 per cent, and then into water, after which the sections were stained in Mayer's Carmalum, ten to fifteen minutes, washed in water and run back through the alcohols, beginning with twenty-five per cent, into absolute alcohol, five

to ten minutes in each. They were then cleared in xylol and mounted in balsam.

In running the sections into and out of the stain (aqueous) the lower grades of alcohol, 25 per cent and 35 per cent, and then water, were necessary, as without their use the transfer into the stain from 70 per cent alcohol was found to be too sudden, causing currents which tore the sections loose from the slide. Any dirt or grease on the slides made this more certain. However, cleaning the latter in 95 per cent alcohol containing a few drops of hydrochloric acid obviated this.

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CONTENTS:

INVESTIGATIONS REGARDING THE PHLOEM AND FOOD-CONDUCTION IN PLANTS, ... *Frank U. G. Agrelius.*

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INVESTIGATIONS REGARDING THE PHLOËM AND FOOD-CONDUCTION IN PLANTS.

BY FRANK U. G. AGRELIUS.

Plates XXXVI-XXXVII.

THIS work is an inquiry into the special devices for the lateral transfer of food materials in the phloëm of vascular plants; to see whether sieve tubes are always present in the higher plants; and to make some comparative studies of the phloëm in stems, petioles and fruitstalks.

At first material in the winter condition was tried but did not prove satisfactory, on account of the difficulty of identifying the sieve tubes in their winter condition. Material was again collected, this time including stems, petioles and fruitstalks, from the spring and summer growth, where the sieve tubes were functioning. Vines were selected at first, from the supposition that the conducting elements would be better developed and therefore plainer. This material was preserved in two-per-cent formaldehyde. As shrinkage of the protoplasm would really assist in making the cell walls more distinct, but little attempt was made to prevent it in the various processes of preparation.

The celloidin method of imbedding was tried at first but it did not serve the purpose well. It was rather essential in the hard material first collected, but the paraffin method worked better in most cases. By the celloidin method slides having the required large number of sections upon them were difficult to make. If the celloidin were left in the sections it stained too much like the cellulose walls. If dissolved out the cuttings were liable to cupping or to injury in the region of the cambium. These facts led to the choice of the paraffin method,

which was used where possible and which proved quite satisfactory in the majority of cases. The oldest material possible was commonly used.

Stains adapted to the work in hand were not found at first. Iodine green and erythrosin were tried, but this method left the phloëm red or pink—a poor color for the purpose. Finally fuchsin for the lignified walls and methyl blue for the cellulose ones were found to be quite satisfactory. The latter gave a fairly dark wall and slime body—the one better for making the drawings, the other rendering the identification of the sieve tubes less difficult.

The sections of such varied kind as to subject and age of material stained quite differently under the same treatment, so that each one usually required some variation. The slides were left in the fuchsin from two hours to several days. The excess stain was removed with acid-alcohol, and the slides were then placed in methyl blue for from twenty seconds to three or four minutes.

As a rule, cross, radial and tangential sections, with many mounts on each slide, were prepared for each subject—in all, more than 300 slides. These included specimens from young and from somewhat older material. The tangential sections proved the best for demonstrating sieve tubes. The cross sections were best for the measurements of cell walls and cell cavities, and to show the locality of the various tissues, etc. All were used to determine, if possible, the presence of pits, or of any other facts bearing on the problem.

PLANTS EXAMINED.

The following is a list of the plants examined, arranged according to the classification of Gray's revised manual:

Pinaceæ:
- Pinus laricio Port.

Alismaceæ:
- Sagittaria latifolia Willd.

Gramineæ:
- Zea Mays Linn.

Cyperaceæ:
- Scirpus validus (Vahl.) L.

Bromeliaceæ:
- Tillandsia usneoides L.

Liliaceæ:
- Yucca glauca Nutt.
- Asparagus officinalis L.
- Smilax rotundifolia L.

Salicaceæ:
- Salix alba, var. vitellina (L.) Koch.
- Populus alba L.
- Populus deltoides Marsh.

Juglandaceæ:
- Juglans nigra L.

Urticaceæ:
- Ulmus fulva Mx.
- Ulmus americana L.
- Celtis occidentalis L.
- Cannabis sativa L.
- Humulus Lupulus L.
- Morus rubra L.

Aristolochiaceæ:
Aristolochia macrophylla Lam.
Aristolochia tomentosa Sims.
Ranunculaceæ:
Clematis Pitcheri T. & G.
Anonaceæ:
Asimina triloba Dunal.
Menispermaceæ:
Menispermum canadense L.
Saxifragaceæ:
Deutzia Fortunei Hors.
Rosaceæ:
Spiræa japonica L. (?)
Pyrus Malus Linn.
Fragaria virginiana Deuchesne.
Rubus occidentalis L.
Rubus cuneifolius Pursh.
Rosa pratincola Greene.
Prunus americana Marshall.
Leguminosæ:
Gymnocladus dioica (L.) Koch.
Gleditsia triacanthos L.
Melilotus alba Desr.
Amorpha fruticosa L.
Desmodium canescens (L.) DC.
Rutaceæ:
Zanthoxylum americanum Mill.
Simarubaceæ:
Ailanthus glandulosa Desf.
Anacardiaceæ:
Rhus glabra L.
Rhus toxicodendron L.
Rhus cotinus L.
Celastraceæ:
Celastrus scandens L.
Aceraceæ:
Acer saccharinum L.
Acer Negundo L.
Rhamnaceæ:
Rhamnus lanceolata Pursh.
Vitaceæ:
Psedera quinquefolia (L.) Greene.
Vitis æstivalis Mx.
Tiliaceæ:
Tilia americana L.
Malvaceæ:
Abutilon Theophrasti Medic.
Cactaceæ:
Opuntia Rafinesquii Engelm.
Haloragidaceæ:
Myriophyllum heterophyllum Mx.
Cornaceæ:
Cornus asperifolia Mx.
Oleaceæ:
Fraxinus viridis Mx. (?).
Syringa vulgaris L.
Asclepiadaceæ:
Asclepiodora viridis (Walt.) Gray.
Asclepias syriaca L.
Convolvulaceæ:
Cuscuta glomerata Choisy.
Labiatæ:
Monarda fistulosa L.
Solanaceæ:
Lycium halimifolium Mill.
Scrophulariaceæ:
Verbascum Thapsus L.
Bignoniaceæ:
Tecoma radicans (L.) Juss.
Catalpa speciosa Warder.
Plantaginaceæ:
Plantago virginica L.
Caprifoliaceæ:
Symphoricarpos orbiculatus Moench.
Triosteum perfoliatum L.
Sambucus canadensis L.
Cucurbitaceæ:
Cucurbita pepo L.
Compositæ:
Brauneria pallida (Nutt.) Britton.
Gaillardia grandiflora ?
Arctium Lappa L.
Cirsium discolor (Muhl.) Spring.
Lepachys pinnata (Vent.)

These range from the Pinaceæ to the Compositæ. They include one parasite, one epiphyte, three hydrophytes and two xerophytes. The list embraces twenty-three herbaceous plants (not including vines), five herbaceous vines, ten shrubby vines, thirteen other shrubs and twenty-one trees. These are em-

braced in thirty-nine families, sixty-five genera, and seventy-two species.

DRAWINGS.

In general, camera-lucida drawings have been made to show the pits in the phloëm when found, to show sieve tubes and some of the adjacent tissues from three points of view. A Bausch and Lomb 1/12 objective was used with but few exceptions, and for measuring a Bausch and Lomb micrometer eyepiece—divisions 1/10 mm. In all about 175 drawings have been prepared for use in evidence.

FINDINGS.

PROBLEM I.—What special devices occur for the lateral transfer of food materials in the phloëm?

After considerable search I have found pits in the lateral walls of the phloëm of fourteen plants, as shown, for example, in figures 1 and 2. In figure 1 they are evidently between the medullary ray and the phloëm; in figure 2, between the sieve tubes and the adjoining cells.

Frank[1] seems to imply that there are no pits between the parenchyma cells of the phloëm. Figure 1 shows some as they appeared between the parenchyma and the parenchyma, and between the parenchyma and medullary-ray cells of the stem of *Populus alba*. He also states that the sieve tubes are the widest phloëm elements.[2] This is hardly true in quite a number of instances, as in *Amorpha fruticosa* (fig. 6), where the parenchyma is the wider. Quoting from Briosi,[3] he states that the slime bodies of the sieve tubes sometimes contain starch granules. Some are shown in figure 7 in *Populus alba*. They were noted also in *Rhus toxicodendron*. Frank states also[4] that the lateral walls of the sieve tubes are never strengthened. Figures 4 and 5 show thickenings on the lateral walls of the sieve tubes in the roots of *Populus deltoides*. It would seem that these are for strengthening the wall. They occur also in the end plates of the sieve tubes of the same plant (figs. 8 and 9) and in *Populus alba*.

Strasburger[5] finds pits between the phloëm parenchyma and the medullary rays. Figures 1, 2 and 3 show such. He also states[6] that the cortical rays are specially adapted by means

1. Frank, A. B.: Lehrbuch der Botanik, 1892, vol. I, p. 184.
2. Loc. cit., p. 183.
3. Loc. cit., p. 183.
4. Loc. cit., p. 183.
5. Strasburger, Ed., Textbook of Botany, 1897, p. 135. (Trans. by Porter.)
6. Loc. cit., p. 135.

of these pits and their contact with the companion cells for taking up and transferring the food materials laterally, especially to the cambium. Figure 6 shows a very common arrangement of the medullary rays which bears out the rest of his statement. It may be added to by saying that the medullary rays are often close to each other tangentially, and the rays and ray-like cells of the pericycle often sweep around the narrow portions of the phloëm, as seen in figure 6 of *Amorpha fruticosa*, as though for the special purpose stated above, and in a way especially fitting them for that function. Some recent research[7] has further verified Strasburger's statements in certain plants.[8]

One thing to be noted in botanical literature is that work on sieve tubes and sieve plates is usually done with plants from the Vitaceæ, Cucurbitaceæ, Tiliaceæ, and a few others, where, as will be seen by reference to table I, the walls of the phloëm are unusually thick. Presumably this is because here the things to be seen are more pronounced, and hence more easily found and studied. Table II shows comparative data collected from the plants having pits in the lateral walls of the phloëm as observed in this work and from those in which such pits were not observed. In *Equisetum* pits are general in the phloëm elements and in the rest of the cortical tissues. In others this is not true. In the tables mentioned it will be seen that pits are present in those plants having thicker walls than those in which pits were not observed, and, as a rule, the sections were from actively functioning tissue. It is seen that the phloëm walls are as thin in some cases as 0.25 micron, and in many cases 0.35 micron. In fact, in the phloëm in many instances there was but little evidence of appreciable addition in thickness to the original vertical wall formed by the cambium or procambium. As a result of this, in drawing with the high magnification of 1200 diameters, it was not feasible to use a double line for representing the thickness of the walls, and the attempt to do so was soon abandoned and choice made of the measurement and tabulation method as shown by the tables. It is quite plain that such thin walls could neither have nor require pits. In the xylem I found pits invariably

7. Hill, A. W., Histology of the Sieve Tubes of Angiosperms. Annals of Botany, vol. 22, No. 86, pp. 246-290.

8. Sykes, M. G., Anatomy and Histology of *Macrocystis pyrifera* and *Laminaria saccharina*. Annals of Botany, vol. 22, No. 86, pp. 291-326.

present, but with the cell walls always much thicker. Even here there are no actual perforations.

Plants often adopt the device of obliquely placed end plates, possibly for the purpose of furnishing greater surface for the pits. This is noticeably true in many instances, especially in the Salicaceæ. As a result it seems necessary to strengthen these walls, and cross banding with thickenings in the walls are seen in figures 2, 8 and 9. The best illustrations (figs. 8 and 9) are from a root of *Populus deltoides*, taken about eight feet below the surface of the ground. Here there is a much increased sieve-plate surface, with strengthening bands at regular intervals, as seen from two directions.

PROBLEM II.—Are sieve tubes always present in the phloëm?

As to this problem, my data, many of which were obtained only after long search, are quite positive. Plants differ greatly in arrangement, location, number, size, staining qualities, etc., of their sieve tubes in the various specimens. However, one can be reasonably sure of their presence by noting the phloëm in cross section. The companion cells and the sieve tubes adjoining form units in outline, which, together with the protoplast of the companion cell and the slime body of the sieve tube, assist in the discovery (fig. 6). Sieve plates are not so easily found, unless it may be in those plants where sieve tubes are numerous, or where one happens to get a section through an unusually favorable place. For still better evidence the slime body is good, but the perforated sieve plate is best. I was usually not satisfied until all of these requirements were met, and the drawings were then made.

Perforations were not found in the end plates in *Pinus laricio*, *Sagittaria*, and *Asparagus*. They were quite numerous, although very small, in *Opuntia*. In *Myriophyllum*, a hydrophyte, they were evident, as in *Cuscuta*, a parasite. In this last were found cells of large dimensions, apparently serving especially as conducting cells. One was 0.1 mm. in tangential diameter by 1.62 mm. in axial length. We could not tell how much longer, because of the limits of the section. Sieve tubes are also present in *Tillandsia*, an epiphite. Here there is a cylinder of sclerenchyma inclosing the vascular bundles, and probably permitting of but little lateral transfer of foods.

Data concerning the sieve tubes are contained in tables I-IV.

It will be seen that the walls are commonly quite thin—those between them and the companion cells being thinnest. Thickness of their walls ranges from 0.25 micron to 4.17 microns.

PROBLEM III.—The facts observed concerning the third part of the problem are tabulated in table III. The tendency is shown to be toward a reduction of the diameter of the vessels in the fruitstalk and petioles, with an increase in thickness of the walls.

RESUME.

First.—There are special devices for the better lateral transfer of foods present in the phloëm and cortex of the plants studied. These are (*a*) pitted walls; (*b*) the arrangement of the phloëm in narrow wedges with pericycle cells sweeping around these and connecting with the medullary rays, and (*c*) radially elongated medullary-ray cells adapted readily to conduct the food as stated. It is probable that in many plants the extreme thinness and large area of the phloëm walls permits a considerable lateral movement of materials without resort to pits, and that no pits are to be found in some (perhaps many) cases.

Second.—Sieve tubes with perforated sieve plates were demonstrated in all but three of the plants examined, and here I was satisfied of their presence. They often increase the area of their sieve plates by placing them obliquely, and these may require special thickenings to support them. The number of the sieve tubes in various species varies considerably. They are present in some plants when probably almost functionless.

Third.—Relatively, the phloëm and xylem do not vary greatly in amount in the various parts of the plants, such as the stems, petioles, etc., but the main differences in this respect are in the other tissues.

TABLE I. Thickness of cell walls in stems (measurements in microns).

	Between adjoining sieve tubes	Between sieve tubes and companion cells	Between sieve tubes and medullary rays	Between tracheal tissues and xyl. parenchyma	Between tracheal tissues and medullary rays
Pinus laricio Bort	0.65	.....	0.65	2.58	1.60
Saggittaria latifolia Willd	0.35	0.32	.....	1.50	.....
Zea mays L	0.50	0.40	.....	1.65	.....
Scirpus validus L	0.30	0.25	.....	1.50	.....
Tillandsia usneoides L	0.30	.....	.....	1.30	.....
Smilax rotundifolia L	1.00	0.60	.....	1.65	.....
Yucca glauca Nutt	0.58	0.40	.....	1.78	.....
Asparagus officinalis L	0.35	0.30	.....	2.79	.....
Salix alba, var. vitellina (L.) Koch	0.40	0.35	0.40	1.85	1.28
Juglans nigra L	0.35	0.30	0.35	2.73	1.65
Populus alba L	1.08	0.53	1.25	2.73	1.65
Populus deltoides Marsh	0.50	0.35	0.50	2.80	1.85
Ulmus Mx fulva	0.35	0.30	0.35	3.53	2.61
Ulmus americana L	0.40	0.35	0.35	3.83	1.67
Celtis occidentalis L	0.35	0.25	0.40	2.31	1.56
Cannabis sativa L	0.35	0.25	0.35	2.60	1.72
Humulus lupulus L	0.30	0.30	.....	3.86	.....
Morus rubra L	0.35	0.30	0.35	2.75	1.60
Asimina triloba Dunal	0.40	0.35	0.55	3.08	.....
Clematis pitcheri T. & G	1.28	0.92	.....	3.72	3.50
Menispermum canadense L	0.45	0.40	.....	2.48	.....
Deutzia fortunei Hort	0.42	0.40	0.35	3.72	2.78
Spiræa japonica L.?	0.35	0.25	0.25	1.58	.....
Pyrus malus L	0.50	0.40	0.55	3.11	1.72
Rubus occidentalis L	0.45	0.45	0.35	2.19	1.75
Rubus cuneifolius Pursh	1.65	1.71	3.30	3.65	1.85
Prunus americana Marshall	0.60	0.40	0.55	2.43	1.92
Gymnocladus dioica (L.) Koch	0.40	0.30	0.45	3.94	3.16
Gleditsia triacanthos L	0.65	0.30	0.58	2.94	2.46
Melilotus alba Desr	0.40	0.25	0.40	3.93	1.85
Amorpha fruticosa L	0.45	0.35	0.40	2.80	1.65
Desmodium canescens (L.) DC	0.40	0.33	0.40	2.70	2.08
Zanthoxylum americanum Mill	0.55	0.35	0.50	3.37	3.25
Ailanthus glandulosa Desf	0.50	0.35	0.45	4.48	3.61
Rhus glabra L	0.75	0.55	0.75	2.64	2.20
Rhus toxicodendron L	0.40	0.35	0.50	1.85	1.35
Rhus cotinus Nutt	0.55	0.55	0.90	2.35	1.50
Celastrus scandens L	0.50	0.38	0.50	3.08	1.85
Acer saccharinum L	0.68	0.55	1.00	2.35	2.00
Acer negundo L	1.00	0.45	0.85	2.60	1.87
Rhamnus lanceolata Pursh	0.50	0.35	0.70	2.50	1.80
Psedera quinquefolia (L.) Greene	0.70	0.50	0.50	2.20	1.85
Vitis æstivalis Mx	2.33	1.72	4.17	3.83	1.77
Tilia americana L	0.55	0.50	1.00	2.48	.....
Abutilon theophrasti Medic	0.65	0.45	0.80	3.25	.....
Opuntia rafinesquii Engelm	0.50	0.38	.....	1.66	.....
Myriophyllum heterophyllum Mx	0.50	0.30	.....	3.10	.....
Cornus asperifolia Mx	0.45	0.25	0.40	3.50	2.08
Fraxinus viridis Mx.?	1.15	0.75	1.30	4.47	2.27
Syringa vulgaris L	0.60	0.40	0.80	2.85	2.02
Cuscuta glomerata Choisy	0.42	0.35	.....	3.40	.....
Lycium halimifolium Mill	0.60	0.35	.....	3.80	.....
Tecoma radicans Juss	0.55	0.40	0.45	3.02	2.13
Catalpa speciosa Warder	0.45	0.25	0.30	2.46	2.15
Sambucus canadensis L	0.50	0.30	0.55	5.56	2.30
Triosteum perfoliatum L	0.60	0.40	0.50	4.44	.....
Symphoricarpos orbiculatus Moench	0.60	0.40	0.50	2.78	1.92
Brauneria pallida (Nutt) Britton	0.65	0.35	.....	2.68	.....
Gaillardia grandiflora	0.50	0.45	.....	3.25	.....
Minimum thickness of wall	0.300	0.250	0.250	1.300	1.280
Maximum thickness of wall	2.330	1.720	4.170	5.560	3.610
Average thickness	0.598	0.430	0.715	2.866	2.095

TABLE II.

	Thickness in microns of walls between—				
	S. t. and s. t.	S. t. and comp. cells.	S. t. and m. ray.	Tracheal tissues and xyl. par.	Tracheal tissues and m. ray.
Pinus laricio Bort	0.65	.....	0.65	2 58	1.60
Yucca glauca Nutt	0.58	0.40	.....	1.78	.....
Salix alba, var. vitellina (L.) Koch	0.40	0.35	0.40	1.85	1.28
Populus alba L	1.08	0.53	1 25	2.73	1.65
Populus deltoides Marsh. (stem)	0.50	0.35	0.50	2.80	1.85
Populus deltoides Marsh. (root)	1.39	1.00	1.22	4.88	3.24
Menispermum canadense L	0.45	0.40	.....	2.48	.....
Rubus occidentalis L	0.45	0.45	0.35	2.19	1.75
Gymnocladus dioica (L.) Koch	0.40	0.30	0.45	3.94	3.16
Celastrus scandens L	0.50	0.38	0.50	3.08	1.85
Psedera quinquefolia (L.) Greene	0.70	0.50	0.50	2.20	1.85
Vitis æstivalis Mx	2.33	1.72	4.17?	3.83	1.77
Abutilon theophrasti Medic	0.65	0.45	0.80	3.25	.....
Symphoricarpos orbiculatus Moench	0.60	0.40	0.50	2.78	1.92
Average for the above plants with pitted walls	0.763	0.556	0.941	2.884	1.993
Average from plants where pits were not observed	0.549	0.394	0.633	2.922	2.133
Difference (+) or (−)	+0.214	+0.162	+0.308	−0.038	−0.140

TABLE III. COMPARISON OF WALL THICKNESS IN STEMS, PETIOLES, AND FRUITSTALKS.
(Measurements in microns.)

	Walls between s. t. and s. t.			Walls between s. t. and comp. cell.			Walls between s. t. and m. rays.			Diameter of sieve tubes.			Walls between tr. and xyl. parench.			Walls between tr. and m. rays.			Diameter of tracheals.			Length of sieve tubes.		
	Stems.....	Petioles.....	Fruitstalks...	Stems.....	Petioles.....	Fruitstalks...	Stems.....	Petioles.....	Fruitstalks...	Stems.....	Petioles.....	Fruitstalks...	Stems.....	Petioles.....	Fruitstalks...	Stems.....	Petioles.....	Fruitstalks...	Stems.....	Petioles.....	Fruitstalks...	Stems.....	Petioles.....	Fruitstalks...
Vitis æstivalis Mx.	2.33	2.37	.....	1.72	2.33	.....	4.17?	2.33	.....	20.83	14.25	.....	3.83	3.09	.....	1.77	2.92	.....	72.90	36.40	.....	.....	.....	.....
Rubus cuneifolius Pursh.	1.65?	1.80	.....	1.71?	1.55?	.....	3.30?	1.50	.....	13.03	8.45	.....	3.65	4.02	.....	1.85	2.24	.....	41.47	28.35	.....	.....	.....	.....
Cannabis sativa L.	0.35	0.35	.....	0.25	0.30	.....	0.35	0.35	.....	18.38	19.89	.....	2.60	3.42	.....	1.72	3.42	.....	33.96	27.70	.....	.....	.....	.....
Rhus glabra L.	0.75	.....	0.50	0.55	.....	0.50	0.75	.....	0.60	12.08	.....	7.83	2.64	.....	2.55	2.20	.....	1.65	32.40	.....	13.75	.....	.....	.....
Desmodium canescens DC.	0.40	.....	0.35	0.33	.....	0.35	0.40	.....	0.35	6.33	.....	4.92	2.70	.....	2.00	2.08	.....	.....	17.43	.....	9.95	.....	.....	.....
Verbascum thapsus L.	0.50	.....	0.50	0.45	.....	0.30	0.45	.....	0.45	12.08	.....	10.96	3.27	.....	3.10	1.83	.....	2.25	33.78	.....	23.81	230.85	.....	.....
Rhamnus lanceolata Pursh.	0.50	.....	0.50	0.35	.....	0.40?	0.70	1.70	0.75	13.16	11.53	5.08	2.50	4.00	3.50	1.80	3.33	2.16	23.76	15.95	15.75	97.6	.....	.....

TABLE IV. *Resume.*
(Measurements in microns.)

	Walls between sieve tubes and sieve tubes.	Walls between sieve tubes and comp. cella.	Walls between sieve tubes and med. rays.	Diameter of sieve tubes.	Walls between tracheals and xyl. parench.	Walls between tracheals and med. rays.	Diameter of tracheals.	Length of sieve tubes.
Stems, only,	0.598[61]	0.430[59]	0.715[45]	12.193[9]	2.866[62]	2.095	33.633[13]	183.608[4]
Petioles, "	1.317[4]	1.093[3]	1.470[4]	13.166[5]	3.526[6]	2.997[3]	30.612[5]	.....
Fruitstalks, only.....	0.504[11]	0.364[7]	0.528[7]	8.302[10]	2.884[11]	2.229[7]	15.830[10]	182.180
Roots, only.	1.390[1]	1.000	1.220	41.640	4.880	3.240	206.55	.....
Minimum...	0.300	0.250	0.250	3.500	1.300	1.280	9.950	97.600
Maximum..	2.330	1.720	4.170(?)	41.640	5.560	3.610	206.55	256.780
Average....	0.622	0.471	0.746	12.009	2.936	2.166	32.845	183.608

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CONTENTS:

HISTOLOGY OF TOWNSENDIA EXSCAPA AND LESQUERELLA SPATHULATA,
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HISTOLOGY OF TOWNSENDIA EXSCAPA AND LESQUERELLA SPATHULATA.

BY LILIAN BUNTON.

Plates XXXVIII to XLV.

TWO excellent representatives of xerophytic vegetation, *Townsendia exscapa* and *Lesquerella spathulata*, were collected in Gove county, Kansas, at an elevation of 2700 feet. These plants are not common throughout this district and are limited to certain localities. *Townsendia* was found growing in draws in the immediate vicinity of the town of Gove and also on the flat, open prairie around "Castle Rock," about twenty-five miles southeast of Gove, and in the vicinity of a group of rocks known as the "Pyramids," thirty miles southwest.

A general idea of the appearance of the vegetation of this district may be derived from figure 1. My examples of *Townsendia*, therefore, were growing on the flat, open prairie as well as in the draws, occurring not in clumps or patches, but as isolated individuals within three or four feet of one another. The plants on the open prairie show a more luxuriant growth than those in the draws.

The specimens of *Lesquerella* were collected about twelve miles southwest of the town of Gove on a rocky, clay bluff. This plant, unlike *Townsendia*, was found growing not as isolated individuals but in rather large colonies.

Of all the ecological factors influencing the structure, habit and distribution of plants the most potent is the water supply. In Gove county the total precipitation for the year 1904 was 18.10 inches; the greatest monthly precipitation was 4.13 inches, in May; the least monthly precipitation was 0 inches in February and November. The total snowfall for the year was 5.5

inches and the number of rainy days 39. In the following table is given the monthly and annual precipitation in Gove county for the year 1904, with departures from the normal:

January.		July.	
Precipitation	0.01	Precipitation	2.18
Departure	—0.57	Departure	—1.47
February.		August.	
Precipitation	0.00	Precipitation	2.57
Departure	—0.72	Departure	+1.11
March.		September.	
Precipitation	1.00	Precipitation	1.26
Departure	+0.32	Departure	—1.08
April.		October.	
Precipitation	1.79	Precipitation	2.00
Departure	—0.27	Departure	+0.98
May.		November.	
Precipitation	4.13	Precipitation	0.00
Departure	+0.89	Departure	—0.51
June.		December.	
Precipitation	2.62	Precipitation	0.55
Departure	—1.25	Departure	+0.03

Annual.
Precipitation 18.10
Departure ..... —2.27

From comparisons with other places in Kansas where weather records have been kept, it is seen that the amount of precipitation of this habitat is remarkably small; in fact, being the least, excepting that of Oberlin, Lakin, and Dodge City, where the annual precipitation was 15.72 inches.

One may acquire a general idea of the temperature of this locality from the following tables:

Monthly and annual mean temperature for year 1904, with departure from normal, Fahrenheit.

January.		July.	
Temperature	29.0	Temperature	74.8
Departure	+0.9	Departure	—3.8
February.		August.	
Temperature	30.6	Temperature	72.6
Departure	+1.9	Departure	—4.0
March.		September.	
Temperature	43.8	Temperature	68.3
Departure	+6.4	Departure	—0.1
April.		October.	
Temperature	48.6	Temperature	55.3
Departure	0.0	Departure	+1.5
May.		November.	
Temperature	57.8	Temperature	44.6
Departure	—4.6	Departure	—0.9
June.		December.	
Temperature	67.4	Temperature	30.2
Departure	—4.9	Departure	—2.4

Annual.
Temperature 51.9
Departure ..... —0.5

Monthly maximum temperatures for the year 1904, with dates.

January 18	65°	July 29	102°
February 9	72°	August 24	95°
March 2	82°	September 9	103°
April 10	79°	October 3	87°
May 24	93°	November 18	73°
June 23	99°	December 31	68°

Monthly minimum temperatures for year 1904, with dates.

January 25	—2°	July 26	54°
February 19	3°	August 22	50°
March 3	6°	September 14	41°
April 17	25°	October 25	25°
May 14	34°	November 11	11°
June 11	50°	December 26	4°

Another ecological factor which has much to do in shaping plants is the wind. On the prairies the wind has full sweep; it blows most of the time at a rapid rate and tends to dry up whatever vegetation there may be in its path. No definite statement can be made as to the velocity of the wind of this special locality. In the following table, however, are shown some of the results of observations made by Stevenson, of Edinburgh, upon the increase in velocity of the wind with the height above the ground, as given in Schimper's Plant Geography:

Height of instrument aboveground, in feet.	Velocity of wind in miles per hour.
½	6.83
2⅓	8.73
4⅓	9.77
9½	10.45
14	10.54
25	11.54
50	12.21

Height of instrument aboveground, in feet.	Velocity of wind in miles per hour.
½	9.8
3½	12.4
9	13.8
14	14.3
25	15.0
51	16.3

Height of instrument aboveground, in feet.	Velocity of wind in miles per hour.
1⅓	22.2
3½	25.6
9	31.9
14	33.7
25	37.1
51	42.7

From the above tabular statement it is quite clear that plants that are only slightly raised aboveground experience the effects of the wind much less than tall plants, and especially trees.

The action of the wind on plants is partly direct by tensile stresses and partly indirect by increasing transpiration; both these actions are the more energetic the taller the plants or the higher their location.

Where my *Townsendias* occurred the soil is a loose, calcareous deposit, allowing the water quickly to percolate through it.

When the character of its habitat is considered, it would be expected that the anatomy of *Townsendia* must be that of a xerophyte.

TOWNSENDIA EXSCAPA.

Townsendia exscapa is perennial from a woody taproot which averages ten centimeters long and three to four millimeters in diameter at the thickest portion. The stem grows from one to four inches high. The fact that this plant is low helps it to endure the strong winds prevailing in its locality.

The character of the stem varies in different plants. In some, while young, it is quite simple, bearing only a few heads of flowers; in others it is several-branched, bearing six or more heads. As a rule, however, it gradually becomes more and more branched with age until the whole plant may attain a breadth of ten to twelve inches, bearing about 100 heads of flowers. The leaves are all clustered at the base, narrowly linear or slightly spatulate, and one to two inches long. The flowers are white and are borne in sessile heads one to one and one-half inches broad. In figure 2 is shown a photograph of *Townsendia*. When the flowers of the larger plants have gone to seed the plants have the appearance seen in figure 3.

In the discussion of the histology of *Townsendia* the stem will be first treated, then the root, and last the leaf, and the different tissue systems under each will be examined.

The Stem.

Tegumentary Tissues.—The protection of the mature stem is provided for by a cutinized epidermis and cork tissue. All the walls of the epidermis are cutinized. In figure 4 is shown a small portion of the cutinized epidermis. In the following table is given the average thickness of the walls of the epidermal cells and the average length and width of the cavity of

the epidermal cells of *Townsendia* and a few mesophytes and xerophytes:

		Outer wall.	Inner wall.	Radial wall.	Vertical length.	Radial width.
MESOPHYTES.	Eupatorium altissimum.	0.005 mm.	0.001 mm.	0.001 mm.	0.022 mm.	0.015 mm.
	Salvia azurea.	0.006 mm. Cutinized portion, 0.005 mm. Cuticle, 0.001 mm.	0.006 mm.	0.003 mm.	0.02 mm.	0.01 mm.
HYDROPHTES.	Sagittaria.	0.003 mm.	0.001 mm.	0.001 mm.	0.02 mm.	0.01 mm.
	Nelumbo-lutia.	0.006 mm.	0.003 mm	0.003 mm.	0.04 mm.	0.02 mm.
TOWNSENDIA.	.....	0.05 mm.	0.02 mm.	0.018 mm.	0.09 mm.	0.068 mm.

In the following table is given the average thickness of the layer of cork, the average thickness of the walls of the cork cells, and the average length and width of the cell cavity in *Townsendia:*

Thickness of cork	4-7	cells.
Average thickness of wall	0.004	mm.
Average length of cavity	0.14	mm.
Average width of cavity	0.087	mm.

In figure 5 is shown a small portion of cork tissue in cross section.

When compared with the mesophytes and hydrophytes above mentioned, it is seen that *Townsendia* has a well developed protective system, one of the primary requisites of a plant growing in a dry, windy habitat.

The Strengthening Tissues.—The strengthening tissues found in *Townsendia* consist exclusively of collenchyma and short sclerenchyma cells. From figures 6 and 7, collenchyma cells as seen in cross and longitudinal sections, it may be seen that the cells of the collenchyma tissue have remarkably thick walls. The walls of the short sclerenchyma cells also are much thickened, as shown in figures 8 and 9. No true bast fibers are found; the tissue that in cross section appeared to be bast when examined longitudinally proved not to be bast, but a tissue of short sclerenchyma cells. Wood fibers are also

wholly lacking. This deficiency, however, is in a measure compensated by the modification of other tissues, the walls of the wood parenchyma, cortex, pith and medullary-ray cells being remarkably thickened. The walls of the cortex and pith cells are, on the average, 0.03 mm. thick. In figures 10 and 11 are shown a few cortex cells as seen in cross and longitudinal sections, respectively. In figures 12 and 13 are shown a few pith cells as seen in cross and longitudinal sections, respectively. As shown in figure 14, the tracheids have thick, lignified walls and constitute the smaller portion of the xylem area; these, together with the wood parenchyma cells, tend to strengthen the plant. A longitudinal section was mounted in a drop of concentrated solution of chromic acid; in a few minutes everything had disappeared but the tracheids. The chromic acid dissolved the wood parenchyma cells, leaving the tracheids isolated as shown in figure 15. The average length of a tracheid is 0.243 mm.; the average width, 0.016. mm.

Tracheal Tissues.—In the stem the conduction of water is provided for by tracheids varying in length, and in longitudinal section having the appearance of typical tracheal tubes. When, however, a longitudinal section was macerated under a cover glass in chromic acid, the tracheids were isolated from the other tissues and stood out prominently as spiral and scalariform tracheids. By computing the number of tracheids in one xylem wedge and multiplying by the number of such wedges, where the cross section of the stem is 19.635 sq. mm. in area, there were found to be 1313 tracheids. The average diameter of these stem tracheids is 0.016 mm. The total water-conducting area of the stem, cross section, is 0.266 sq. mm., which is 1.3 per cent of the whole stem. Of the xylem portion of the stem, 6.6 per cent is given up to tracheids.

When compared with the water-conducting tissue of several mesophytic herbaceous plants, that of *Townsendia* seems quite small. In *Saponaria officinalis* 22.7 per cent of the whole stem is devoted to the conduction of water; of the xylem portion 29 per cent, the average diameter of a tracheal tube being 0.026 mm. Thus it is seen that 17 times as much of the stem of *S. officinalis* as in *Townsendia* is devoted to the conduction of water.

In *Verbena stricta* there was devoted to the conduction of water 9 per cent of the stem cross section, where the area was

found to be 3.801 sq. mm. Of the xylem portion, 62 per cent was devoted to the conduction of water. In *Verbena,* then, there was found devoted to the conduction of water seven times as much of the stem as in *Townsendia.* In *Mentzelia oligosperma* there was devoted to the conduction of water 9 per cent of the stem cross section, where the area was 9.07 sq. mm. Of the xylem portion, 33 per cent was devoted to the conduction of water. In *Mentzelia* also there was found to be devoted to the conduction of water nearly seven times as much of the stem as in *Townsendia.* In *Ambrosia artemisifolia* there was found devoted to the conduction of water 21 per cent of the stem cross section, where the area was 13.86 sq. mm. Of the xylem portion 52 per cent was devoted to the conduction of water. In *Ambrosia,* then, there was devoted to the conduction of water about sixteen times as much of the stem as in *Townsendia.* In *Abutilon avicennæ* there was devoted to the conduction of water 2 per cent of the stem cross section, where the area was 38.48 sq. mm. Of the xylem portion, 6 per cent was devoted to the conduction of water. In *Abutilon,* accordingly, there was devoted to the conduction of water approximately twice as much of the stem as in *Townsendia.*

When compared with the water-conducting tissues of desert plants, which have have been discussed by W. A. Cannon[1] in his paper on the "Water-conducting Systems of Desert Plants," *Townsendia* has a relatively large water-conducting area.

In the following table is given the number of tracheal elements in 1 sq. mm. of stem, cross section, of *Townsendia,* and of several mesophytes and xerophytes; the latter cited from Cannon:

Townsendia	66
Mesophytes:	
Abutilon avicennæ	33
Verbena stricta	734
Mentzelia oligosperma	77
Ambrosia artemisifolia	124
Xerophytes:	
Celtis pallida	1
Covillea tridentia	2
Fouquieria splendens	7

Tissues for Food Conduction and Storage.—The medullary ray is composed of two kinds of cells, some with rather thick

1. Bot. Gazette, June, 1905, pp. 396-408.

cellulose walls which measure 0.001 mm. in thickness. The thick-walled medullary-ray cells constitute approximately one-third of the whole area of a medullary ray. An explanation of there being both thick- and thin-walled medullary-ray cells may possibly be that the thick-walled cells have sacrificed their function of conduction and have assumed that of strengthening. The average vertical length of a medullary-ray cell is 0.01 mm.; the average width 0.008 mm. In figure 16 are shown a few medullary cells as seen in cross section; in figure 17 as seen in longitudinal section.

Very little special provision for the passage of food longitudinally seems to have been made by *Townsendia*. The ordinary collateral vascular bundles are found. A comparatively small portion of the vascular bundle, however, is devoted to phloëm—about 12 per cent; in *Verbena stricta* 25 per cent of the vascular bundle is devoted to phloëm. In *Mentzelia oligosperma* there is the same proportion of the vascular bundle devoted to phloëm as in *Townsendia*—12 per cent. Neither sieve tubes nor sieve parenchyma cells are found in *Townsendia*. The whole work of conduction of food longitudinally is apparently assumed by the cambiform cells and the undivided mother cells of the sieve tubes. Presumably the sieve tubes, when present in a plant, would carry the food more rapidly. The most elaborated sieve tubes are always found in plants of considerable length, especially in trailing, clambering and climbing plants. *Townsendia*, however, is so low that it seems that the food can be conducted longitudinally rapidly enough and in sufficient quantities by the cambiform and undivided mother cells of the sieve tubes without the aid of sieve tubes.

In figure 18 are shown phloëm cells as seen in cross section; in figure 19, as seen in longitudinal section: *a*, cambiform cell; *b*, undivided mother cell of the sieve tubes. The average length of these cells is 0.18 mm; the average width, 0.01 mm. The average thickness of their cell wall is 0.0006 mm.

In *Townsendia*, the xylem parenchyma cells and the medullary ray, cortex and pith cells afford sufficient means for the storage of food. Upon examination of sections of the stem of the plant collected at the time of flowering and fruiting, there appeared stored up in the tissues of the stem no food whatever, thus showing that the food must at this time be used

by *Townsendia* as fast as it is made. No statement, however, can be made of the storage of food in the plant later in the season.

The Root.

Tracheal Tissues.—As in the stem, the conduction of water in the root is provided for by spiral and scalariform tracheids. By computing the number of tracheids in a certain portion of a cross section, and multiplying by the number of such portions, there were found to be 1271 tracheids in the cross section of the root. In figure 20 may be seen how these tracheids are distributed throughout the section. The average diameter of these tracheids is 0.018 mm. The total water-conducting area in a root, where the cross section area is 7.496 sq. mm., is 0.325 sq. mm., or 4.2 per cent of the whole root area.

In structure, the other tissues of the root do not differ essentially from those of the stem; hence the discussion of them as found in the stem will suffice for the root.

The Leaf.

The Tegumentary Tissues.—The outer wall of the epidermis of the leaf is not wholly cutinized; the inner portion is of cellulose and is 0.0108 mm. thick, and the outer portion of the wall is cutinized and is 0.0072 mm. thick. The inner tangential wall is of cellulose and is 0.0036 mm. thick. The radial walls are likewise of cellulose and 0.0036 mm. thick. The average tangential length of the cells of the epidermis is 0.0396 mm.; the average radial length, 0.025 mm. No difference was found between the upper and lower epidermis, hence the figures given above will suffice for both. In figure 24 is shown a portion of the cutinized epidermis as seen in cross section.

Tracheal Tissues.—After a leaf boiled in alcohol had remained in a mixture of chloral hydrate and hydrogen peroxide for several days, it had become so well bleached that its venation could be seen easily with the naked eye. There appeared three prominent longitudinal veins, one central and two lateral, from which extended other veins branching in every direction and terminating in water-storage tracheids, as shown in figure 21*a*. In the cross section of the midrib through the center of the leaf were found ninety-five tracheids, the average diameter of which was 0.0075 mm., making the

total water-conducting area there 0.00004 sq. mm. The cross-section area of the midrib was 0.01207 sq. mm., 32 per cent of which was devoted to conduction of water. In figure 21*b* is shown the midrib as seen in cross section. In the cross section of each of the lateral veins were found twenty-eight tracheids, the average diameter of which was 0.0059 mm., making the total water-conducting area in each vein 0.00073 sq. mm. The total cross-section area of each vein was 0.003 sq. mm., 24 per cent of which was devoted to the conduction of water. The average distance between the ultimate branches of the veins—*a* and *b*, figure 22—is 0.031 mm.

In the leaf, the phloëm consists only of cambiform cells and undivided mother cells of the sieve tubes; the xylem is made up of wood parenchyma cells and spiral and scalariform tracheids. The average diameter of the cavity of the tracheids is 0.006 mm. The walls of the parenchyma cells, however, remain quite thin. In figure 23 are shown the phloëm cells as seen in longitudinal section of the midrib: *a*, cambiform cell; *b*, undivided mother cell of the sieve tubes. The average length of these cells is 0.14 mm., the average width 0.01 mm., the average thickness of the cell wall 0.0006 mm.

The Photosynthetic Tissues.—On both sides of the leaf are found palisade cells; the spongy parenchyma cells are not very prominent and towards the center of the leaf, in some places in the leaf not really being differentiated from the palisade cells. The explanation of the palisade cells on both sides of *Townsendia* may be that out on the open prairie the reflected light from below is sufficiently intense to stimulate the formation of palisade tissue on the under side of the leaf.

On each side of the leaf there are from two to three layers of palisade cells, the average length of which is 0.14 mm., the average width 0.05 mm. The average number of chloroplasts in a single cell is twenty-nine and the average diameter of a chloroplast is 0.0008 mm. In figure 25 are shown the palisade cells as they appear in surface view; in figure 26 spongy parenchyma cells as they appear in surface view.

In the following table is shown the number of chloroplasts

found in a single mesophyll cell of a number of plants, as given in Haberlant's "Pflanzen-Anatomie":

	Palisade cells.	Spongy parench. cells.
Fragaria elatior	86	14
Pulmonaria officinalis	85	15
Ricinus communis	82	18
Brassica rapa	80	20
Galeopsis tetrahit	79	21
Tropaeolum majus	77	23
Helianthus annuus	73	27
Phaseolus multiflorus	69	31
Bellis perennis	67	33

When compared with the plants above mentioned, it is seen that in the leaf of *Townsendia* the chloroplastic surface is relatively small. On both sides of the leaf the number of chloroplasts in a single mesophyll cell is approximately twenty-nine, thus giving to both sides of the leaf the same chlorophyll-producing volume. The small number of chloroplasts found in the mesophyll cells of the upper side allows the sunlight to penetrate to the lower side of the leaf, thus giving to the cells there the power to carry on photosynthesis more effectively.

The Water-storage Tissues.—In the leaf of *Townsendia* there is an admirable arrangement for all the mesophyll cells to have immediate access to water. Throughout the full length of the leaf on both sides are found large cells which are used primarily for the storage of water. These water-storage cells, however, seem to assume other functions; they evidently take part in the conduction of water and aid to a slight degree in photosynthesis. They have very thin walls, which are lined by a few chloroplasts much smaller than those found in the other mesophyll cells. Bordering on these water-storage cells are mesophyll cells which draw upon them for water when there is need.

In order to secure the greatest access to water the palisade cells occur in various relations: bordering on veins, on water-storage cells, on spongy parenchyma cells. In the following table is shown the relative frequency of palisade cells bordering respectively on water-storage cells, veins and spongy parenchyma cells:

Bordering on water-storage cells	222
Bordering on veins	81
Bordering on spongy parenchyma cells	42

From the above figures it is seen that the palisade cells occur most frequently bordering on the water-storage cells, there being nearly three times as many bordering on the water-storage cells as on the veins and twice as many bordering on the veins as on the spongy parenchyma cells. Figure 27 is a diagrammatic drawing, showing the distribution of water-storage cells, *b*, as seen in a cross section of a leaf. In figure 28 are shown the palisade cells, *B*, bordering on water-storage cells, *A*. In figure 29 are shown the palisade cells, *A*, bordering on the veins, *C*. Some places in the leaf the palisade cells, *D*, have still greater access to water, bordering as they do on both water-storage cells, *A*, and storage tracheids, *C*. This relation generally occurs at the ends of the leaf. In figure 30 are shown the palisade cells as found in this relation. Sometimes the palisade cells are found bordering on water-storage cells, *A*, which in turn border on veins, *C*, as shown in figure 31. Such an arrangement as this is an excellent one; for as fast as the water-storage cells are deprived of the supply of water on hand they can immediately draw on the veins and thereby continue to supply the palisade cells with water as it is needed. In figure 32 are shown palisade cells, *A*, bordering on spongy parenchyma cells, *B*.

Another means for storage of water is the water-storage tracheids found at the termination of the veins. Palisade cells bordering on these tracheids can obtain water when there is need. In figure 33 are shown these tracheids as they appear at the ultimate ends of the veins; in figure 34 the water-storage tracheids as they appear in other places in the leaf.

The Aërating Spaces.—In *Townsendia* there were found devoted to aëration only 20 sq. mm. of the surface of a leaf which measured 100 sq. mm.; or, in other words, the volume of the intercellular spaces and the volume of the whole leaf, roughly estimated, stand in the relation to each other as 8:1000. When compared with *Pistia texensis*, an hydrophyte, whose aërating volume and the volume of the whole leaf stand in the relation to each other as 760: 1000, the amount of volume devoted to aëration in *Townsendia* seems quite small.

There were found on either side of the leaf an approximate average of 344 stomata to 1 sq. mm., the average number usually found in plants. There was no difference in the char-

acter of the stomata on either side of the leaf. It seems rather surprising to find in the leaf of a xerophyte the usual number of stomata found in plants and to find them at the surface of the leaf instead of being sunken beneath the epidermis; for, as a rule, in xerophytic plants there are fewer stomata and they are often sunken beneath the epidermis.

In figure 35 are shown the stomata as they appear in the surface view of the leaf of *Townsendia*. In figure 36 is shown a stoma as it appears in cross section of the leaf.

SUMMARY.

1. *Size and Habit of Townsendia.*—*Townsendia* is a low plant, growing from one to four inches high; it grows on the flat, open prairie as well as in the draws, and occurs not in clumps but as isolated individuals. The stem is at first relatively simple, but, as a rule, it becomes more and more branched with age until the whole plant may attain a breadth of ten to twelve inches.

2. *Tegumentary Tissues.*—In the mature stem of *Townsendia* the cutinized epidermis, whose outer walls measure 0.05 mm., and the cork tissue several layers thick, constitute the tegumentary tissues.

In the leaf of *Townsendia* there is found an epidermis whose outer wall measures 0.017 mm. in thickness. The outer portion of the wall is cutinized and measures 0.0072 mm. in thickness; the inner portion is of cellulose and measures 0.0108 mm. in thickness.

3. *Strengthening Tissues.*—In *Townsendia* the strengthening tissues of the stem consist of collenchyma and short sclerenchyma cells. True bast fibers and wood fibers are lacking. The remarkably thick cell walls, not only of the strengthening tissues but of nearly all the tissues, make the stem of *Townsendia* strong.

4. *Tracheal Tissues.*—The area devoted to conduction of water in *Townsendia* is comparatively small, there being only 1.3 per cent of the stem devoted to that function. Growing as it does in a location where the water supply is poor, *Townsendia* would not require very extensive water-conducting tissues.

5. *Food-conducting Tissues.*—Longitudinally there seems to have been made very little provision for the conduction of

food in the stem. The phloëm portion is very little differentiated; it consists only of cambiform cells and undivided mother cells of the sieve tubes, there being found neither sieve tubes nor sieve parenchyma cells.

6. *Storage Tissues.*—Since *Townsendia* grows in a xerophytic habitat it is not surprising to find in it some provision for the storage of water. In the stem, the cortex, medullary ray and pith cells are well adapted to the storing of water. In the leaf, however, special provision is made: throughout the whole length of the leaf are found large water-storage cells which not only reduce transpiration but also rapidly fill whenever the water supply is increased, and yield their contents to the assimilating cells as the supply of water there is reduced.

7. *Aërating Spaces.*—As would be expected to be found in a xerophyte, the amount of space devoted to aëration is comparatively small. Only one one hundred and twenty-fifth of the volume of the leaf of *Townsendia* is devoted to aëration; while in *Pistia* about two-thirds of the volume of the leaf is thus employed.

LESQUERELLA SPATULATA.

Lesquerella spatulata is perennial by a much branched caudex which varies from one to two inches in length. It has a taproot which measures from one foot to a foot and a half in length and one-fifth of an inch in diameter at its thickest portion. The leaves are separated by short internodes and appear tufted. They measure from one-half to one inch in length and one-fifth to one-seventh of an inch in width. They are entire and vary in form from narrowly elliptic to ovate-lanceolate, oblanceolate and spatulate, and they, as well as the pedicels, are beset with stellate hairs. The flowers are yellow and are borne on pubescent scapes which measure from one-half inch to six inches in length.

The Stem.

The Tegumentary Tissues.—The protection of the mature stem is provided for by a cutinized epidermis and cork. There is, in addition to these tissues, in older portions of the stem, a borke. All of the walls of the epidermis are cutinized. Figure 37 represents a small portion of the epidermis as seen in cross

section; figure 38*a*, a small portion of the epidermis as seen in longitudinal section.

In the following table is given the average thickness of the cell walls and the average length and width of the epidermal cells:

Outer tangential wall	0.0049 mm.
Inner tangential wall	0.0049
Radial wall	0.003
Vertical diameter of cavity	0.075
Radial diameter of cavity	0.026
Tangential diameter of cavity	0.04

In the following table is given the average radial breadth of the cork zone, the average thickness of the walls of the cork cells, and the vertical, radial, and tangential dimensions of the cell cavity:

Average breadth cork zone	15-20 cells.
Average thickness of wall	0.001 mm.
Vertical diameter of cavity	0.025
Radial diameter of cavity	0.026
Tangential diameter of cavity	0.036

Figure 38*b* represents a few cork cells as seen in cross section.

In addition to this large zone of cork there are found in the borke rather large stone cells, which, as shown in figure 39, have relatively thick and pitted walls.

The tegumentary tissues are remarkably well developed for such a low, herbaceus plant as *Lesquerella*. When, however, its xerophytic habitat is taken into consideration, the necessity for this provision is readily seen.

The Strengthening Tissues.—The strengthening tissues in the stem consist of collenchyma, bast fibers, stone cells and wood fibers.

The radial breadth of the collenchyma zone is 0.093 mm. The average thickness of the walls of the collenchyma cells is 0.006 mm.; the average tangential breadth of the cell cavity is 0.036 mm.; the average radial thickness is 0.01 mm. In figure 40 are shown a few collenchyma cells as seen in cross section; in figure 41 as seen in longitudinal section.

The sclerenchyma tissue is made up of cells which vary from stone cells to short bast fibers. As shown in figure 42, the stone cells found here are smaller than those found in the borke. Figure 43 represents the stone cells as they appear in longitudinal section.

The bast fibers are 0.11 mm. long and 0.016 mm. wide, the average thickness of the cell wall being 0.006 mm. As may be seen in figure 44, the ends of the fibers overlap but little. In figure 45 are shown a few bast fibers as seen in cross section.

The most striking characteristic of the strengthening tissues of the stem is the presence of large zones of thick-walled wood fibers, which constitute 26 per cent of the area of the stem and 78 per cent of the area of the xylem. These wood fibers, as shown in figure 46, occur among spiral tracheal tissues. They average 0.11 mm. in length and 0.01 mm. in width. The walls are remarkably thick—0.006 mm.; the cell cavity is exceedingly small, in some places being almost entirely obliterated. Figure 47 represents a wood fiber as seen in longitudinal section.

The strengthening system in the stem of *Lesquerella* is more extensively developed than that in the stem of *Townsendia*, the only strengthening tissues found in the stem of *Townsendia* being collenchyma and short sclerenchyma cells, bast fibers and wood fibers being absent. This deficiency in *Townsendia*, however, is compensated by remarkably thick cell walls, not only of the strengthening tissues but of nearly all the tissues. The strengthening tissues in the stem of *Lesquerella* are so well developed that there is no need of the other tissues being modified, as was the case in the stem of *Townsendia*.

The Tracheal Tissues.—The tracheal system in the stem of *Lesquerella* consists of spiral and scalariform tracheal tubes and spiral and scalariform tracheids alone. There was found devoted to the conduction of water 2 per cent of the stem cross section, where the area was 7 sq. mm.; 4 per cent of the xylem, where the cross section area was 3.46 sq. mm., was devoted to this purpose.

In the following table is given the average thickness of the cell wall, and the average tangential and radial dimensions of the cell cavities of the various tracheal elements found in the stem of *Lesquerella*:

	Average thickness of cell wall.	Radial diameter of cavities.	Tangential diameter of cavities.
Largest tracheal tubes	0.002 mm.	0.016 mm.	.....
Smallest tracheal tubes	0.003	0.002	.....
Tracheids	0.002	0.016	0.04 mm.

As shown in figure 46—a small portion of the xylem as seen in cross section—the tracheal elements occur among alternating, definite zones of wood fibers, *A*, and wood parenchyma

cells, *B*, the largest ones being among the wood fibers and the smallest among wood parenchyma cells. It is generally conceded that spiral vessels are formed by the procambium exclusively, and wood fibers by the cambium. As the tracheal elements found interspersed among the wood fibers are spiral and scalariform, the activity here must be due either to the cambium or procambium. From the fact that these spiral vessels are found somewhat remote from the pith, there follows a probable conclusion that the cambium, contrary to the general rule, has formed spiral vessels.

The tracheal elements found in the stem at the nodes were different from those in the internodes. At the nodes the tracheal tissues consist exclusively of short and peculiarly shaped tracheids. In figure 48, *A*, are shown the scalariform type of tracheids; *B*, the spiral type of tracheids as seen in longitudinal section.

In the internodes the tracheal elements consist exclusively of spiral and pitted tracheal tubes, with the exception of a few tracheids interspersed here and there. Figure 49, *A*, illustrates the spiral tracheal tubes found among the wood fibers, as seen in longitudinal section; figure 49, *B*, spiral tracheal tube found among the wood parenchyma cells; figure 49, *C*, pitted tracheal tubes as seen in longitudinal section.

Tissues for the Conduction and Storage of Food.—The medullary rays found in the stem of *Lesquerella* present an interesting characteristic. Throughout the entire length of the medullary ray are found leaf traces containing spiral tracheal tubes as shown in figure 51, *a*. These tracheal tubes are much smaller than those found in the xylem area of the stem, the average diameter of the cavity being 0.007 mm. and the average thickness of the cell wall 0.002 mm. Figure 50, *a* represents a leaf trace. The internodes are so short that it is impossible to cut a section without having leaf traces traversing the medullary rays. These leaf traces run horizontally into the primary xylem, and when the cambium begins its activity it builds up the medullary rays around them. The average width of a medullary ray is 0.06 mm., and the average vertical length of a medullary-ray cell is 0.03 mm., and its average width is 0.01 mm. Figure 51, *b* represents a small portion of the medullary ray as seen in cross section.

In the stem, the ordinary collateral vascular bundles are

found; 20 per cent of the vascular bundle is devoted to phloëm, as in *Townsendia*. Neither seive tubes nor seive parenchyma cells are found. The whole work of conduction is assumed by the undivided mother cells of the sieve tubes. *Lesquerella* is a very low plant and it seems that the food can be conducted longitudinally fast enough and in sufficient quantities without the aid of the other phloëm elements. In figure 51, *c*, are shown a few phloëm cells as seen in cross section; in figure 52, as seen in longitudinal section; at the angles of these cells occur small intercellular spaces, *A*.

In the stem of *Lesquerella* the storage of food is provided for by means of the thin-walled parenchyma of the cortex and the xylem parenchyma and the medullary rays. Figure 53 represents a few cells of the thin-walled parenchyma of the cortex as seen in cross section. Figure 54 represents a few cells of the xylem parenchyma as seen in longitudinal section. In all of these tissues starch and proteid were found in small quantities, but neither sugar nor oil.

Figure 50 is a diagrammatic drawing of the cross section of the stem traced as seen when projected upon a screen. From this may be derived a general idea of the various tissues of the stem, their relation to one another, and the proportion of the stem devoted to each: *A*, borke; *B*, collenchyma; *C*, sclerenchyma; *D*, phloëm; *E*, xylem; 1, tracheal tissues; 2, wood fibers; 3, xylem parenchyma; *F*, medullary ray; *a*, leaf-trace.

The Root.

The Tegumentary Tissues.—The tegumentary tissues of the mature root consist of a cutinized epidermis and cork tissue which are similar to those tissues found in the stem, both in structure and proportion.

The Strengthening Tissues.—The strengthening tissues found in the root of *Lesquerella* consist of collenchyma, stone cells and wood fibers. These tissues show no difference whatever from those found in the stem.

The Tracheal Tissues.—The tracheal tissues in the root consist entirely of scalariform and spiral tracheal tubes. In a root where the cross section area was 18.75 sq. mm., there was found devoted to the conduction of water 4 per cent. Here the cross-section area of the xylem is 6.7 per cent of the entire root.

In the following table is given the average diameter and the

average thickness of the cell walls of the tracheal elements in the root:

Average diameter of the larger tracheal tubes	0.03 mm.
Average diameter of the smaller tracheal tubes	0.007
Average thickness of cell wall	0.005

As in the stem the tracheal elements of the root are interspersed among definite, alternating layers of wood fibers and wood parenchyma cells. Figure 55 represents a few wood fibers and tracheal tubes as found in the outermost layer of xylem (fig. 56*a*, *E*) as seen in cross section. Here the tracheal tubes are relatively large and the wood fibers have comparatively large cavities. The next succeeding layer of xylem (fig. 56*a*, *F*) consists of very small, thick-walled tracheal tubes, *A*, and wood parenchyma cells, *B*, shown with greater magnification in figure 57. In figure 58 are shown a few wood parenchyma cells as seen in longitudinal section. The average length of these cells is 0.07 mm. and the average width 0.015 mm. Figure 59 represents a few wood fibers and tracheal tubes found in the next succeeding layer of xylem (fig. 56*a*, *G*). The average diameter of the tracheal tubes in this layer of xylem is 0.023 mm.; here the wood fibers have remarkably thickened walls and a smaller cavity than those found in the outermost layer of xylem (fig. 56*a*, *E*).

Figure 56*a*, a segment of the cross section of the root, shows the constitution of the xylem: *A*, wood fibers; *B*, tracheal elements; *C*, wood parenchyma.

In figure 56*b* are shown the tracheal elements found in the root: *A* and *B*, scalariform tracheal tubes, *C*, spiral tracheal tube.

Tissues for the Conduction and Storage of Food.—In the root are found only secondary medullary rays, which are narrower than those found in the stem. In these medullary rays is found no tracheal system as in those of the stem. As in the stem, there seems to have been made very little provision for the passage of food longitudinally. Yet, however, a larger proportion (25 per cent) of the vascular bundle of the root is devoted to phloëm than in the stem. The phloëm consists exclusively of undivided mother cells of the sieve tubes.

Starch and proteids in small quantities were found in the medullary rays and phloëm-parenchyma cells, but neither glucose nor oil. In the root of *Townsendia* there was found glucose, but neither starch, proteid nor oil.

In figure 60—a diagrammatic drawing of the cross section of the root traced as seen when projected upon a screen—are shown the different zones of tissues of which the root consists and their relation to one another: *A*, cork; *B*, collenchyma; *C*, stone cells; *D*, thin-walled parenchyma; *E*, phloëm; *F*, wood fibers; *G*, wood parenchyma; *H*, tracheal elements; *I*, medullary ray.

The Tegumentary Tissues.—The tegumentary tissues consist of an epidermis with trichomes. All the walls of the epidermis are cellulose except the outer tangential wall, which has a thin film of cutin on the outer portion. The outer and inner tangential wall each measures in thickness 0.006 mm., and the radial wall 0.003 mm. The average radial diameter of the cell cavity is 0.02 mm., the average tangential diameter 0.016 mm. On both sides of the leaf the epidermis is of the same character. Figure 61 represents a small portion of the epidermis: *a*, cutinized portion; *b*, cellulose portion. The trichomes are thickly distributed over both sides of the leaf, and must be quite effective in giving protection. The discussion of these trichomes will be taken up in connection with the water-storage system.

The Tracheal Tissues.—For the study of venation, a leaf was used which had been bleached by standing four or five hours in dilute hydrochloric acid and then two or three days in chloral hydrate. As shown in figure 62, there could be seen in this leaf one large central vein, *A*, running longitudinally throughout the length of the leaf and sending off near the center of the leaf two large lateral branches, *B*, and below the center the large branch, *G*. On either side of the midrib there are two prominent longitudinal veins, *C*. These primary veins send out other veins which branch in every direction and end abruptly, as shown at *D*. The average distance between the ultimate branches of the veins, *E* and *F*, is 0.16 mm., there being included within this area, on the average, twenty-five mesophyll cells. The phloëm consists only of undivided mother cells of the sieve tubes, whose average length is 0.16 mm. and width 0.006 mm. The xylem consists exclusively of spiral tracheary tracheids. The average diameter of the tracheids in the midrib is 0.006 mm., and the average diameter of those in the smaller veins is 0.003 mm. In the midrib, where the cross-section area is 0.015 sq. mm., 20 per cent is devoted to

the conduction of water. Figure 63 represents a small portion of the midrib as seen in longitudinal section: *A*, spiral tracheary tracheid; *B*, undivided mother cell of the sieve tubes.

The Photosynthetic Tissues.—The leaf of *Draba* is bifacial, that is, palisade cells occur on both sides of the leaf, which is from twelve to fifteen layers of cells thick. The average radial length of a palisade cell is 0.027 mm., the average cross diameter 0.02 mm. Figure 64 represents a few palisade cells as seen in surface view.

The average number of chloroplasts in a single mesophyll cell on either side of the leaf is twenty-seven. The small number of chloroplasts found in the mesophyll cells of the upper side of the leaf allows the sunlight to penetrate to the lower side, thus giving to the cells there the power to carry on photosynthesis effectively.

The Water-storage Tissues.—In the leaf of *Lesquerella* there are no water-storage cells as are found in that of *Townsendia*. The only structures in the leaf that might serve principally as water-storage elements are the large trichomes which occur on both sides of the leaf. These trichomes, as shown in figure 65 (surface view) are quite frequent, and are stellate-peltate in form. These, as a rule, are found above a vein, and, since they are alive even on old leaves, they presumably have some active function to perform. Their basal portion is slightly depressed beneath the lower level of the epidermis, and the wall here is cellulose. The remaining portion of the wall of the trichomes is cellulose, except the very outer portion, which is cutinized. The fact that these trichomes occur above the veins and that their basal portion is cellulose-walled seems to point to the conclusion that when there is plenty of water furnished by the veins they absorb water, store it up, and yield it to the mesophyll cells as it is needed. Figure 66 represents a trichome as seen in a leaf cross section: *A*, cutinized portion of a wall of trichome; *B*, cellulose portion of wall of trichome; *C*, mesophyll cells; *D*, tracheids.

The Aërating Spaces of the Leaf.—Mounting the bleached leaf so that it could be looked through from surface to surface, I estimate that approximately 2.7 per cent of the volume of the leaf is devoted to intercellular spaces; in other words, the volume of the intercellular spaces and the volume of the whole leaf, roughly estimated, stand in relation to each other as

27 : 1000. On either side of the leaf are found 640 stomata to 1 sq. mm., a much larger number than was found in the leaf of *Townsendia*. The stomata are at the surface of the leaf instead of being sunken, as is often the case with xerophytes. In figure 67 are shown a few stomata as seen in surface view. In figure 68 is shown a stoma as seen in cross section.

Figure 69 represents a small portion of a leaf as seen in cross section: *A*, upper epidermis; *B*, lower epidermis; *C*, palisade tissue; *D*, vascular bundle.

SUMMARY.

1. *Size and Habit of Lesquerella spathulata.—Lesquerella spathulata*, a perennial from a branched caudex, is a low plant growing from one to two inches high. It was found growing on a rocky clay bluff, occurring not as isolated individuals, but in colonies.

2. *Tegumentary Tissues.*—In the mature stem of *Lesquerella* the tegumentary tissues consist of a cutinized epidermis, cork, and borke. In the mature root the tegumentary tissues consist of a cutinized epidermis and cork.

The tegumentary tissues of the leaf consist of an epidermis, all the walls of which are cellulose except a thin film of cutin on the outer tangential wall. There is, in addition to the ordinary epidermal cells, stellate trichomes on both sides of the leaf, which would be effective in protection against too intense illumination and in the reduction of transpiration, as well as in the storage of water.

3. *The Strengthening Tissues.*—The strengthening tissues consist of collenchyma, bast fibers, stone cells and wood fibers. The wood fibers constitute a very important part of the strengthening system. These have remarkably thickened walls, the cavities in some cases being almost obliterated. Contrary to the general rule, the wood fibers are found among spiral tracheal tubes, both wood fibers and spiral tracheal tubes having been formed by the cambium.

4. *Tracheal Tissues.*—The tissues devoted to the conduction of water constitute 2 per cent of the stem and 4 per cent of the root. This seems a comparatively small area devoted to this purpose, but growing, as *Lesquerella* does, in a location where the water supply is poor, it would not require very extensive

water-conducting tissues. The tracheal tissues consist of spiral and scalariform tracheal tubes and tracheids.

5. *Photosynthetic Tissues.*—The photosynthetic tissues of the leaf consist exclusively of palisade cells, and there is found in a single palisade cell on either side of the leaf an average of twenty-seven chloroplasts.

6. *Food-conducting Tissues.*—As in *Townsendia,* the phloëm is but little differentiated. It consists exclusively of undivided mother cells of the sieve tubes; sieve tubes and sieve parenchyma cells are wholly lacking.

7. *Storage Tissues.*—In the stem the phloëm cells and medullary-ray cells afford provision for the storage of food. In these tissues starch and proteids were stored up in small quantities. The only storage tissues found in the leaf are the large stellate hairs which, possibly, rapidly fill whenever the water supply is increased, and, being cellulose-walled at their bases, yield their contents to the mesophyll cells as the supply of water is reduced.

8. *Aërating Spaces.*—As would be expected to be found in a xerophyte, the amount of space devoted to aëration is comparatively small, there being only 2.7 per cent of the volume of the leaf devoted to this purpose.

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NOTICE TO EXCHANGES.

The attention of learned societies and other institutions which exchange scientific publications with the University of Kansas is called to the list of publications of this University on the third page of the cover of this issue.

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CONTENTS:

Cell Changes in the Alveoli of a Carcinoma of the Mamma,
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THE KANSAS UNIVERSITY SCIENCE BULLETIN.

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CELL CHANGES IN THE ALVEOLI OF A CARCINOMA OF THE MAMMA.

BY EARL F. CLARK.

(Contribution from the Zoölogical Laboratory, No. 188.)

Submitted in partial fulfillment of the requirements for the degree of Master of Arts.

Plates XLVI to XLVIII.

THE literature upon the pathological new growths of the human body scarcely mentions amitosis as a method of cell increase. It occurred to me to treat in a comparative way the two methods of cell division, mitosis and amitosis, as they are found in neoplastic material.

It is not intended to make this paper conclusive, but to make it the first of a series of case studies from the results of which a general conclusion may be deduced as to the relative importance of indirect and direct cell division in these new growths.

I am indebted to Dr. M. T. Sudler for the following history: "In the first week of October, 1907, she fell, bumping the breast against a hard object. No further notice was taken of the incident, however, until the latter part of November, when she noticed a hard, thin, round lump in the right breast about the size of a silver dollar. It was then freely movable. About the 25th of December she noticed a tingling in the right arm, and on January 1, 1908, the arm began to ache. The original mass increased rapidly in size until the whole breast was involved. Its rate of growth seemed intermittent, some weeks being much more rapid than others. Upon examination the entire breast was found to be occupied by a hard, firm mass, which was intimately incorporated in the connective tissue of

the breast. The nipple was somewhat retracted but not completely. The mass was movable over the muscle. The axillary nodes were enlarged and hard. On February 5 the breast, together with the axillary lymph nodes, was removed. On March 13 a recurrence in the left breast was discovered, which was removed on March 20. Twelve days later metastatic nodules in the neck were removed. The patient died soon afterwards from an apparently general carcinomatous involvement of the body. From the foregoing history it is plain that this was an extreme type of the most rapidly growing and malignant of tumors."

This material was not prepared especially for fine cytological work because the discovery of its excellence for investigation was not made until after its fixation. It was fixed in ten-percent formalin and remained in a weaker solution until used. I found the cell nests somewhat shrunken away from the surrounding stroma and the chromatin either so swollen or so poorly preserved that I was unable to make out details in regard to the chromosomes. The fixation otherwise was good. The tissue was mounted in paraffin and cut in sections eight micra thick. Sections were stained in hæmatoxylin for twelve hours after being in a mordant of iron-alum for twelve hours. They were then decolorized in the iron-alum solution to the desired extent.

The cells studied appeared in variously shaped pockets or alveoli surrounded by dense white fibrous connective tissue. This connective tissue stroma was penetrated more or less by columns of tumor cells, one to three cells in diameter. In short, this specimen in parts conformed to the scirrhus while in others it was more of the medullary type of carcinoma. In this paper I will confine my study to the cell nests or alveoli.

In the first four figures I chose a typical field from widely separated parts of the tumor for each drawing, and drew all the structures appearing in that field. I did this to show the similarity of the cell content of the tumor mass throughout. The normal resting cell, with its variation in size, shape and chromatin content, composed the greater number of cells of each group. It was considered the normal resting cell because of its uniform staining quality, its maintenance of cell and nuclear wall, its content of regularly outlined chromatin nucleoli within a single nucleus. Marked variation in any of these

characteristics was considered a cell change having as its ultimate end either the production of new cells or degeneration.

Among the resting cells were others which could be easily identified as being in the process of indirect division. Although no detail of the chromosomes could be made out, yet the increased amount of chromatin over the resting cell, its affinity for the stain, the irregular outline of the chromosomes, the absence of the nuclear membrane and the shape and position of the chromatin masses identical with those of the prophase, metaphase, anaphase, and telophase leave no doubt as to the identity of such cells. Equally distributed among the resting cells were other cells which were clearly abnormal, owing to their unusual size and their content of two or more nuclei or clefts of greater or less depth which either separated or tended to separate the single nucleus into two or more distinct segments. These separated segments had all the characteristics of the nucleus of the resting cell. I have considered such cells as in the process of direct cell division, although I have been unable to find a single cell showing distinct separation of the cytoplasm. Adami thus describes amitosis: "The nucleus divides without any apparent preliminary rearrangement of its structure. It becomes elongated, then dumb-bell shape (the process can be followed in the amœba), the connecting neck becomes broken across and the two daughter nuclei pass apart, their separation being in some cases followed by division of the cell body while in others this further division is wanting and the binucleate cell is produced." Patterson, in "Amitosis in the Pigeon's Egg," says: "In most cases the nucleus elongates in the direction transverse to the plane of the future division, after which a constriction in the nuclear membrane appears about the entire circumference of the nucleus. This constriction continues to deepen until a complete division is effected. A modified form of this type is found in those cases in which the constriction proceeds from one side."

Although the process in this material differs somewhat, I think, from that described by Adami and Patterson for other material, the result is the same. Therefore I feel safe in assuming that cells with the nucleus wholly or in various degrees of separation are in the process of amitosis. Ziegler and Vom Rath consider such cells as already in the process of degeneration. If so, it will not be out of place to consider along with these division figures structures that appear throughout

this material and which are plainly cells in varying degrees of degeneration, as evidenced by changes in the chromatin, cytoplasm and cell wall, and note if there is any similarity between them.

Figures 5, 6, 7 and 8 are used to further illustrate these three cell changes as they appear in various parts of the tumor. In these drawings I omitted the greater number of the resting cells.

I will supplement this preliminary account by short descriptions of individual cells in the several plates with interpretations of their variation from the normal.

I have used the term "cell nests" to mean the group of cells within the alveoli; the term "chromatic cells" to mean those cells in that condition in the degeneration process just before the chromatin loses its staining power and when it has swollen so much and become so diffuse as to fill the entire nucleus as a more or less densely staining mass.

OBSERVATIONS.

The Cells of the Nests Change by Mitosis, Amitosis and Degeneration.

In showing the cell changes of these nests I will simply use a number of figures, describing each one with some amount of detail and inserting comments as observations suggest.

FIGURE 1 is drawn from cell nest 2. It includes three cells dividing directly, one dividing indirectly, two cells in the process of degeneration, and a number of resting cells.

The resting cell is smaller than the dividing cell, is of polyhedral shape, has a limiting membrane, and a large, well-marked nucleus. Its cytoplasm is denser than the karyoplasm and is of a reticular appearance. The nucleus has a well-marked nuclear wall and usually contains from one to three regularly round, deeply-stained chromatic bodies which I will call chromatin nucleoli. A directly dividing cell is of much larger size than the resting cell and usually a bit clearer, a condition suggesting that it has included a large amount of fluid preparatory to its division. The nucleus divides by the formation of a groove or cleft on one side. I have not seen a cell where the cleft appeared on the two sides. The cleft deepens and the nuclear substance pulls apart to form the regular outline of the daughter nuclei. The nuclear membrane seems to follow the deepening cleft so that as soon as the segments have separated the karyoplasm is enclosed by its wall.

In the cells shown I have drawn them as they appeared in outline in one plane, but included the chromatin through the depth of the cell. Each well-defined segment of the nucleus usually contains a chromatin nucleolus. In cell *A* the lower nuclear segment has a second cleft appearing upon its inner border. Cell *B* has two distinct nuclear segments, each one of which has a secondary groove appearing upon its upper surface. The upper segment shows no chromatin at all. Cell *C* shows two nuclear segments, each containing a chromatin nucleolus. Cell *D* shows a central constriction of its nucleus with the mother chromatic mass in the plane of constriction, but I do not say it is in the process of division.

Cell *E* is a representation of the typical indirect division figures found in this material. It is in the early anaphase. As I have already said, this material, being fixed in formalin with no particular care regarding its cytological preservation, shows no detail characteristics of the chromosomes. I have used in my counts only the well-marked division figures, from the close spireme stage on. In these indirect divisions the cells are larger than the resting cells, the nuclear membrane had disappeared, and about the chromatic figure the cytoplasm was clear. I was unable to make out the spindle or any of the details farther than shown.

Cells *F F* are two fragments of degenerated cells in each of which the chromatin has swollen and coalesced into one homogeneous, deeply staining mass.

FIGURE 2. Among the cells of this group there is not the noticeable difference in size usually seen between the dividing cells and the resting ones. Cell *A* shows an indirect division plainly. Cell *B* shows the nucleus being divided by a cleft passing in from its upper surface. Each segment contains a chromatin nucleolus. Cell *C*, an otherwise ordinary resting cell, contains in its cytoplasm, half way from the cell border to the nuclear membrane, a clear vesicle, regular in outline and with a definite limiting border indicating that it is filled with a substance differing from the cytoplasm.

FIGURE 3 shows no new structures, but attention is called to the regularity of the chromatin nucleoli. Cells *A* and *B* show the nuclei entirely segmented and each segment containing regular chromatin nucleoli, the lower segment of cell *B* containing two.

FIGURE 4 is a group of twelve tumor cells drawn from cell nest 1, a small nest of seventy-five cells containing six indirect and no direct divisions. In this group are shown four of the six indirect divisions. Cells *A* and *B* are noticeable for their large size, while cells *C* and *D* are of the same size as the resting cells. Cell *E* is a common-sized resting cell, containing one chromatin nucleolus but with a hollow clear vesicle bulging into the wall of its nucleus. Cell *F* is a common resting cell except that it has its chromatin diffused through the karyoplasm.

FIGURE 5. In this group and in those following I have not included all the cells that appeared in the field, but simply instructive ones and enough resting cells to show a comparison. The group was drawn from cell nest 3, of 253 cells, which included six indirect and five direct divisions. Cell *C* was in the fourth tier from the edge and on the peripheral side of the group. It was large, being .0125 mm. in its greatest diameter and showing a nucleus in two segments, each segment containing a regularly round chromatin nucleolus. The cell was noticeably clearer than the others. Cell *B* also has a bisegmented nucleus, but its chromatin was scattered in irregular masses through the karyoplasm. It was also large, being .01 mm. in its greatest diameter. The nucleus of cell *A* was in three segments, each part having a regularly round chromatin nucleolus, and beside this a certain amount of chromatin scattered in clumps through the karyoplasm. It was .0125 mm. in its greatest diameter. In all my cell measurements I used a micrometer scale which I have found by measurement to give the following dimensions: With a drawing board on a level with the object and at the same inclination as the microscope stage, using 1/12 oil-immersion objective and a 8× Huyghenian ocular, an object that fills the square of the scale is .0125 mm. in diameter; with the 1/6 objective it is .03 mm. in diameter, and with a 2/3 objective it is .15 mm. in diameter. Three-fourths of the square equals .0093 mm.; one-fourth of the square is equal to .0031 mm.; one-half of the square is equal to .0062 mm. Cell *D* is in the indirect division process. Cell *E* is a structure that is common among the tumor cells and I have concluded that it is a degeneration result, although it may occur anywhere in the cell nest among the otherwise vigorous cells. It is characterized by a large amount of deeply staining chromatic material, homogeneous and closely massed, having

no definite form but with a more or less regular outline. This mass evidently represents the nucleus, which has become filled with a diffused, swollen mass of chromatin. Its cell membrane has broken down, allowing the cytoplasm to flow out into the surrounding intercellular spaces. Notice the regular form of the chromatin nucleoli in this group of cells.

FIGURE 6. This group of eleven cells was drawn from the same cell nest as the previous group. Cell *A* is a large cell, .0093 mm. in its greatest diameter. In the cytoplasm about the nucleus are four vesicles, similar to those described under figures 2 and 4. The chromatin of its nucleus is of regular outline but is unusual on account of its size, being a trifle over one-half the diameter of the nucleus itself, at least twice the amount found in the ordinary resting cell. I think it is a cell just beginning the degeneration process shown by the swelling of its chromatin. Cell *C* is undoubtedly in the process of degeneration, for its cell membrane has disappeared, allowing the cytoplasm to flow out uncontrolled. It is a cell almost as large as cell *A*. Its chromatin, which exists as a deeply staining mass somewhat irregular in outline, was larger in diameter than that of cell *A*. The nuclear wall could not be made out. Cell *B* is one farther along in the process of breaking up than cell *C*, for most of its cytoplasm has gone. The diameter of its chromatic element is not so much larger than that of cell *C* but it is more condensed and of more regular outline. These three cells, I think, are respectively in advancing stages of disintegration. Cell *D* is a cell dividing indirectly, having a chromatic mass larger than that of cell *C* but of a looser arrangement, indicating individual chromosomes. It also maintains its cell borders perfectly.

FIGURE 7. This group of eleven cells was drawn from cell nest 6 in the region of a necrotic area. Cells *A* and *B* are in the fifth and sixth tiers respectively from the free edge of the tumor on the peripheral side of the group. I will use this group and the one following it, figure 8, to show changes in the cells passing inward from the free edge of the cell nest to a necrotic area. On the side peripheral to cell *A* there is a small necrotic spot two or three cells in diameter, which accounts for cells *A* and *B* on that side of the group. Cell *A* is a good specimen of such cells as *C* and *B* of figure 6 or cell *E* of figure 5. It shows the swelling of the chromatin and the disin-

tegration of the cytoplasm well. While there has been a swelling of the chromatin in each of these cells there has been an equally great shrinkage of the nucleus, so that at this stage there has been a real loss of material to the nucleus. Cell *B* is peculiar in that its nucleus, while practically the same size as normal, stains very dark; not solid, as in *A*, but granular. There is also a faint indication of its chromatin nucleolus remaining, not indicating so much that it has become diffused through the karyoplasm as that the karyoplasm itself assumes a new staining power. The cell wall of cell *B* is broken down in one place, showing signs of disintegration. Cell *C*, a directly dividing cell, is .0093 mm. in its greatest diameter, while cell *D* is just a trifle less than .0125 mm. The average diameter of the resting cells of this group is near .007 mm. So I think that a cell preparing for direct division increases in size to a marked extent.

FIGURE 8. This group of sixteen cells is taken from cell nest 6, the same nest that group 7 is taken from, and drawn from a zone of cells to the inner side of group 7, that is, between group 7 and a necrotic core which lies in the central part of the nest. These two figures show well the transition from the more peripheral nondegenerating cells to the entirely necrotic mass of cell debris which fills the central portion of so many of the cell nests. No dividing cells were shown. Cell *A*, the most peripheral of the group, is the only one showing a chromatin nucleolus. It is an ordinary resting cell. In cells *B* and *B'*, a type of many cells found at this zone about the necrotic area, and for that reason described as characteristic, no chromatin nucleolus could be made out through the depth of the cell, but in each of these the chromatin was scattered through the karyoplasm in the form of a loose network, staining lightly. The cell and nuclear membranes were preserved perfectly. Passing inward toward the center of the nest is a field of cells which I have called "chromatic cells," and which are perfectly characteristic of a zone of cells that immediately surrounds the necrotic core of the cell nest. They are a transition stage between the normal cells and the wholly degenerated ones. They resemble closely the disintegrating cells described in figures 5, 6 and 7, but seem to have another history of formation. As in the other cells, the nucleus is filled with a homogeneous chromatic mass, the outer layers staining darker

than those farther toward the center. In this field the stain was not as intense as that in the cells of the previous figures but was of a grayish shade, and passing toward the necrotic area the light in the gray increases until in cells *D* and *D'* there is just enough black remaining to outline the nucleus well. From this stage it gradually fades out until the cells are entirely necrotic and do not stain at all. The cell membrane in this group could not be decided upon satisfactorily. In cells *A*, *B* and *B'* it was perfectly intact, while in cells *E* it seemed to be entirely gone. In other cells, as *C*, *C'*, the cell outline was definitely preserved, while yet again in cells *D* and *D'* the cell boundary was irregular and indefinite. But I am safe in saying that when the cell has so far degenerated that the color has disappeared from the nucleus the cell membrane has also disappeared and disintegration immediately follows. But in many of these cells the cell membrane has at least partially gone while the chromatin stains deeply. The nucleus of cell *B'* is 0.004 mm. in diameter while the chromatin mass of cell *C* is near 0.003 mm. in diameter, showing an appreciable shrinkage of this element in the degeneration process.

The Mitotic Divisions Occur in General Upon the Periphery of the Alveolus, the Amitotic Nearer the Center.

I will use camera lucida drawings, together with tables, to prove this. I counted the number of cells, the number of direct divisions and the number of indirect, and also counted the tier of cells from the periphery of the cell nest in which each division occurred. I hoped by this method to arrive at some conclusion as to the rapidity of growth of the tumor, in order to compare it later with the growth of the adult and embryonic mammary tissue. I also wished to decide as to the relative frequency in occurrence of the direct and indirect divisions and to note, if possible, whether there was any comparison between the relative proportions of these and the sort of nests in which they occurred. I also wished to decide if there was a well-founded relation between either of these methods of cell division and the necrotic areas indicating that one or the other was related to degeneration, or that they occurred equally in the same region showing that they were equally vital methods of cell growth.

Cell Nest 2 was the non-necrotic limb of a necrotic body. It was counted up to the beginning of the necrotic area. I can-

not give the tiers of cells in which the various divisions occurred in this nest.

No. of cells.	*Direct divisions.*	*Indirect divisions.*
563	9	16

Percentage	of cells in divisions	4.42
"	of cells in direct divisions	1.50
"	of cells in indirect divisions	2.90
"	of divisions which are direct	36
"	of divisions which are indirect	64

CELL NEST 3. This nest apparently is a small nest in diameter but it has four "chromatic cells," which indicates that it is somewhat degenerating.

Tier	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*Total*
Direct D.	.	.	.	2	1	.	.	.	2	..	..	6.2	5
Indirect D.	3	1	.	1	1	.	.	.	.	..	..	2.3	6

No. of cells.	*Direct divisions.*	*Indirect divisions.*
253	5	6

Percentage	of cells in divisions	4.34
"	of cells in direct divisions	1.90
"	of cells in indirect divisions	2.40
"	of divisions which are direct	45.40
"	of divisions which are indirect	54.50

CELL NEST 4. This was a nest with a necrotic center .125 mm. to .1125 mm. in diameter, while around this on the edge of the nest was a zone of cells varying in width from .05 mm. to .037 mm. which was undegenerate and which constituted the number of cells counted, so that the total number of cells counted does not show the real size of the nest in point of number of cells, one-half of the area of the nest being degenerate.

Tier	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*Total*
Direct D.	1	.	3	1	2	1	1	1	.	1	1	5.5	12
Indirect D.	.	1	2	1	1	.	1	1	.	1	.	5.2	8

No. of cells.	*Direct divisions.*	*Indirect divisions.*
515	12	8

Percentage	of cells in divisions	3.88
"	of cells in direct divisions	2.30
"	of cells in indirect divisions	1.50
"	of divisions which are direct	60
"	of divisions which are indirect	40

CELL NEST 5. This was one of the smaller sized nests and was quite vigorous, showing no degenerating cells at all.

Tier	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*Total*
Direct D.	.	.	.	.	.	.	.	.	.	..	..	00	00
Indirect D.	3	.	.	1	.	.	.	.	.	..	..	1.7	4

No. of cells.	*Direct divisions.*	*Indirect divisions.*
106	00	4

Percentage of cells in divisions	3.77
" of cells in direct divisions	0
" of cells in indirect divisions	3.77
" of divisions which are direct	0
" of divisions which are indirect	100

CELL NEST 6. This was a cross section of a large alveolus, being .2875 mm. in length and .1758 mm. in width. It was regularly oval in outline. There were two degenerate spots in it at opposite sides, the size of six to eight cells. With these exceptions the cells were all counted.

Tier	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*Total*
Direct D.	.	1	4	1	.	3	.	2	1	..	..	5.0	12
Indirect D.	.	1	1	.	.	.	.	2	.	..	..	5.2	4

No. of cells.	*Direct divisions.*	*Indirect divisions.*
676	12	4

Percentage of cells in divisions	2.36
" of cells in direct divisions	1.70
" of cells in indirect divisions	0.60
" of divisions which are direct	75
" of divisions which are indirect	25

CELL NEST 7. This was a small, oval, non-necrotic nest.

Tier	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*Total*
Direct D.	.	.	.	.	.	.	.	.	.	..	..	00	00
Indirect D.	1	4	.	.	.	.	.	.	.	..	..	1.8	5

No. of cells.	*Direct divisions.*	*Indirect divisions.*
123	00	5

Percentage of cells in divisions	4.06
" of cells in direct divisions	0
" of cells in indirect divisions	4.06
" of divisions which are direct	0
" of divisions which are indirect	100

CELL NEST 9. This was a large necrotic nest, .2125 mm. in diameter, with a necrotic center .1125 mm. in diameter, which had a border of vigorous cells .05 mm. wide.

Tier	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*Total*
Direct D.	1	.	4	.	1	1	.	.	.	1	..	4.2	8
Indirect D.	1	.	1	.	.	.	.	.	.	..	..	2.0	2

No. of cells.	*Direct divisions.*	*Indirect divisions.*
299	8	2

Percentage of cells in divisions	3.34
" of cells in direct divisions	2.60
" of cells in indirect divisions	0.70
" of divisions which are direct	80
" of divisions which are indirect	20

In the following cell nests I have taken the serial sections of the same nest and counted them in the same way as I did the single sections of the previously counted nests. I hope in this way to in a manner corroborate my results and also to study the history of the cell nest farther.

CELL NEST 10. This nest was .4125 mm. in length, .0875 mm. in width. It was a nest that showed occasional spots of six to eight cells that had broken down, an average of two of these spots in each nest. The direct divisions occurred largely in the upper, wider end, while the indirect occurred largely in the lower, narrower end, but I have not illustrated this by sketches. It was therefore taken as a nest, non-necrotic, but near the stage when it would rapidly have become so, indicated by the degenerate spots.

CELL NEST 10, A.

Tier.	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*D.D.*	*I.D.*	*Cells.*
Direct D.	.	.	1	2	1	2	1	.	.	1	..	5.6	8	..	...
Indirect D.	1	6	2	3	.	2	.	.	.	..	..	3.0	..	14	532

CELL NEST 10, B.

Direct D.	1	1	2	5	1	2	.	.	.	..	..	4.2	12	..	...
Indirect D.	2	3	3	3	.	.	.	.	.	..	..	2.6	..	11	600

CELL NEST 10, C.

Direct D.	.	3	1	.	.	3	.	.	.	..	..	3.8	7	..	...
Indirect D.	2	2	.	3	2	.	.	.	.	..	..	3.1	..	9	557

CELL NEST 10, D.

Direct D.	.	1	1	3	2	2	1	.	.	..	..	4.6	10	..	...
Indirect D.	2	3	2	2	.	.	.	.	.	..	..	2.4	..	9	655

CELL NEST 10, E.

Direct D.	.	.	3	2	2	1	1	.	.	..	..	4.4	9	..	...
Indirect D.	1	1	2	1	1	1	.	.	.	..	..	3.4	..	7	654

CELL NEST 10, F.

Direct D.	.	.	4	3	2	2	.	.	.	..	..	4.1	11	..	...
Indirect D.	2	2	3	4	.	2	1	.	.	..	..	3.5	..	14	650

CELL NEST 10, G.

Direct D.	.	.	1	.	.	4	2	.	.	..	..	5.8	7	..	...
Indirect D.	3	7	2	1	.	1	1	.	.	..	..	2.6	..	15	564

No. of cells.	*Direct divisions.*	*Indirect divisions.*
4212	64	79

Percentage of cells in divisions	3.39
" of cells in direct divisions	1.50
" of cells in indirect divisions	1.80
" of divisions which are direct	44
" of divisions which are indirect	56

The direct divisions averaged 1.68 rows nearer the center than the indirect divisions.

CELL NEST 11. This nest was probably one-half of a half necrotic alveolus. A sketch of it in cell nest 11 *A* is given in figure 9. The cross-hatched area shows that part of the nest that is necrotic, while the white border about it is the area of the cells counted.

CELL NEST 11, A.

Tier.	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*D.D.*	*I.D.*	*Cells.*
Direct D.	.	2	.	1	.	.	.	.	.	..	..	2.6	3	..	...
Indirect D.	.	1	.	2	.	.	.	.	.	..	..	3.3	..	3	334

CELL NEST 11, B.

Direct D.	.	3	.	1	.	3	.	1	.	1	..	5.1	9	..	...
Indirect D.	2	.	1	.	.	.	.	.	.	..	..	1.6	..	3	305

CELL NEST 11, C.

Direct D.	.	.	.	1	1	3	.	1	.	..	..	5.8	6	..	...
Indirect D.	1	4	.	1	.	1	.	.	.	..	..	2.7	..	7	279

CELL NEST 11, D.

Direct D.	1	.	2	1	1	2	1	.	.	..	..	4.3	8	..	...
Indirect D.	1	2	1	.	.	.	.	.	.	..	..	2.0	..	4	296

CELL NEST 11, E.

Direct D.	.	1	1	.	2	.	.	.	1	.	..	4.8	5	..	...
Indirect D.	1	1	.	1	1	.	.	.	.	..	..	3.0	..	4	279

CELL NEST 11, F.

Direct D.	.	.	1	.	1	.	1	.	.	1	..	6.2	4	..	...
Indirect D.	2	.	2	.	.	3	.	.	.	..	..	3.7	..	7	271

CELL NEST 11, G.

Direct D.	.	2	1	1	3	.	.	1	1	1	..	5.3	10	..	...
Indirect D.	3	1	.	.	1	.	.	.	.	..	..	2.0	..	5	404

CELL NEST 11, H.

Direct D.	.	2	2	1	.	.	1	.	1	..	..	4.2	7	..	...
Indirect D.	.	3	1	1	1	.	.	.	.	..	..	3.0	..	6	391

CELL NEST 11, I.

Direct D.	.	.	2	.	2	2	.	.	1	1	..	5.8	8	..	...
Indirect D.	.	3	1	2	2	.	1	.	.	..	..	3.6	..	9	393

CELL NEST 11, J.

Direct D.	.	1	.	.	.	.	2	.	.	..	..	5.3	3	..	...
Indirect D.	1	.	1	3	1	.	.	.	.	..	..	3.5	..	6	306

No. of cells.	*Direct divisions.*	*Indirect divisions.*
3258	63	54

Percentage of cells in divisions	3.59
" of cells in direct divisions	1.90
" of cells in indirect divisions	1.60
" of divisions which are direct	53.80
" of divisions which are indirect	46.10

The direct divisions in this nest averaged 2.1 rows farther away from the free edge of the nest than the indirect, or 2.1 rows nearer the center of the nest.

Cell Nest 8. The work upon this nest was done with greater care than that upon the previous nests. I first made a camera lucida sketch of the nest in outline, then went over the nest carefully with the high power 8x compensating ocular and marked each division I found upon the outlined sketch. I then used an 8x Huyghenian ocular, upon the diaphragm of which I had placed a micromillimeter scale, and went over the field again, carefully counting the cells by the aid of the micrometer scale, and verified the previous locations of the dividing cells and located any new ones that I may have missed in the first survey. I thus corroborated my work and made it doubly sure by locating each dividing cell upon an outline sketch. I also used these sketches in the hope that together with the tables I might farther establish the apparent relation of directly dividing cells to the degenerating areas. Where this relation has been especially noticeable I have made high-power camera lucida drawings of the particular field to show some detail about the cells I counted, simply drawing the more important structures in relation to them. Using these large drawings and marking their position upon the smaller sketches one cannot avoid showing in the same way the slide does the real relation of the various dividing cells to these necrotic areas. In these outline sketches I only outlined the nest, tracing into any irregularities among the cells along the edge, so that, unless otherwise marked, rifts in the nests will mean spaces left where the cells have apparently been pulled apart by external means. The areas that are entirely necrotic will not be distinguished from those that show definite degenerating changes; cells that are in the "chromatic cell" stage I have counted as necrotic. These areas are shown by cross-hatched work. The indirect divisions are shown by a dot or "×" while the direct divisions are shown by a circle. Starting with figure 10 the sections are in serial arrangement. This cell nest 8 is only a portion of the entire alveolus, showing at the right side of the sketch just the end of a necrotic plug, and leaving the greater part shown in the vigorous condition. I used this nest to contrast, if possible, the two divisions in these two areas.

FIG. 10. CELL NEST 8, A.

Tier.	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*D.D.*	*I.D.*	*Cells.*
Direct D.	.	1	.	1	3	.	.	2	1	..	..	5.4	8	..	...
Indirect D.	2	4	4	1	2	2	.	.	.	..	..	3.2	..	15	534

FIG. 11. CELL NEST 8, B.

Direct D.	.	1	2	3	2	.	1	.	.	..	..	4.1	9	..	...
Indirect D.	1	4	4	3	1	2	.	.	.	..	..	3.3	..	15	511

FIG. 12. CELL NEST 8, C'.

Direct D.	.	1	1	1	5	1	3	2	1	..	..	5.7	15	..	...
Indirect D.	7	3	3	3	2	1	4	1	.	..	..	3.5	..	24	554

FIG. 14. CELL NEST 8, C.

Direct D.	.	1	2	2	2	2	.	1	.	..	..	4.6	10	..	...
Indirect D.	2	2	2	5	2	1	1	1	.	..	..	4.0	..	16	555

CELL NEST 8, D.

Direct D.	1	2	.	1	2	3	2	.	.	..	..	5.1	11	..	...
Indirect D.	3	1	3	3	4	1	1	.	.	..	..	3.6	..	16	626

SUBNEST 8, D.

Direct D.	.	.	.	1	1	.	.	.	.	..	..	4.5	2	..	...
Indirect D.	3	5	1	.	.	.	.	.	.	..	..	1.7	..	9	172

CELL NEST 8, E.

Direct D.	.	1	2	2	3	2	.	.	.	..	1	4.9	11	..	...
Indirect D.	4	3	7	4	4	.	.	.	.	..	..	3.0	..	22	869

CELL NEST 8, F.

Direct D.	.	.	3	2	6	2	3	.	.	..	..	5.0	16	..	...
Indirect D.	3	5	3	2	2	2	.	.	.	..	..	3.0	..	17	745

FIG. 16. CELL NEST 8, G.

Direct D.	.	2	3	1	3	4	1	1	.	..	..	4.7	15	..	...
Indirect D.	2	6	2	1	.	1	1	.	.	..	..	2.8	..	13	916

FIG. 18. CELL NEST 8, H.

Direct D.	1	2	3	1	.	3	3	.	.	..	..	4.3	13	..	...
Indirect D.	3	1	7	1	.	.	2	.	1	..	..	3.5	..	15	907

FIG. 19. CELL NEST 8, I.

Direct D.	1	.	2	1	2	.	1	3	.	..	1	5.7	11	..	...
Indirect D.	1	1	7	2	4	1	1	.	.	..	..	3.8	..	17	912

No. of cells.	*Direct divisions.*	*Indirect divisions.*
7301	121	179

Percentage of cells in division	4.01
" of cells in direct division	1.60
" of cells in indirect division	2.40
" of divisions which are direct	40.33
" of divisions which are indirect	59.66

The direct divisions of this nest averaged 1.78 rows nearer the center than the indirect.

DESCRIPTION OF OUTLINE SKETCHES AND DRAWINGS.

CELL NEST 8, "A" (fig. 10). The amount of necrotic material in this figure is greater than in the following ones, the necrotic plug showing less and less in each consecutive section. There are no divisions shown in this figure near the necrotic plug, but the nearest two are direct. The greater part of the dividing cells are in the limb of the nest.

CELL NEST 8, "B" (fig. 11). The number of divisions present in the distal part of the limb is noticeable. There are three direct divisions immediately adjacent to the necrotic plug and one nearer than the nearest indirect division.

CELL NEST 8, "C" (fig. 12). In this nest there was an unusually large number of dividing cells. At the point of the arrow in figure 12 is the center of the group of cells drawn on a large scale in figure 13. About the arrow point are the four direct divisions and the two indirect divisions shown in the enlarged group. This group of nineteen cells includes a larger area under the lens than any previously drawn. I drew all the cells of importance under the field of the camera lucida, including a field .05 mm. in diameter, while the previous groups drawn have included an area only .0375 mm. in diameter. It is located on the edge of the necrotic area and includes the whole width of cells lying between this area and the free edge of the cell nest, cell *F* being in the first row of the nest, while cell *B* is among the necrotic cells. The direct divisions of this section are deep in the center of the nest, while the indirect are largely very close to the edge, seven cells out of twenty-five dividing indirectly lying in the first row and no directly dividing cells nearer than the second row, and then only one. A general survey of these sketches together with the tables strongly indicates that the cells on the edge of the tumor increase almost, if not wholly, by indirect divisions, while those deeper away from the edge increase largely by direct divisions but occasionally by indirect. I want to emphasize by the large drawings the intimate association of the directly dividing cells with the degenerate ones. Cells *H*, *H'*, *H"* are the "chromatic cells" that I have described previously under figure 13. Surrounding these cells closely are cells *A*, *B*, *C*, *D* and *E*, plainly in the process of direct division. Cell *B* is peculiar in that it shows no chromatin nucleolus in either segment of the nucleus. This same occurrence was noticed in numbers

of resting cells, *B*, *B'*, figure 8, etc., just outside the zone of "chromatic cells" *H*, *H'*, *H''*. Its chromatin had wholly or largely disappeared, and if any remained it was loosely diffused through the karyoplasm. Cell *E* is another cell showing no chromatin in any of the segments of its nucleus. It evidently was in decay for it was very translucent. The fragments of its nucleus showed no chromatin at all. It may be that a cell such as *B*, which has vigor enough to cause its nucleus to segment but not to cytoplasm, gradually loses its staining ability and its definiteness of outline and later becomes merely a mass of debris through a stage represented in cell *E*. Cells *F* and *G* are two cells in the indirect division process. The directly dividing cells are much larger than the resting cells or those dividing indirectly. Cell *A* is .0093 mm. in its greatest diameter, cell *B* is .007 mm., cell *C* is .0093 mm., cell *G* is .0062 mm., cell *F* is .0062 mm., cell *E* is .0093 mm., cell *D* is .0085 mm., while cell *I*, an average resting cell, is .0062 mm. in its greatest diameter. This cell shows the breaking up of the chromatin and its diffusion through the karyoplasm, possibly preceding cells *H*, *H'*, *H''*. Its nucleus is .005 mm. in diameter, while the diameter of the "chromatic mass" in cells *H*, *H'*, *H''* is .0031 mm., showing evidently a shrinkage in the latter.

FIGURE 14. In this section two indirect divisions are shown located on the very edge of the necrotic plug, and two more near. There are also close to the edge of the nest three direct divisions, still showing a greater proportion of direct divisions near the necrotic area than indirect, when compared with the total number of divisions of each in the section. But this shows that indirect division may occur on the very edge of a degenerating area.

At the lower extremity of the limb of the regular section following is found a circular group of cells, which in the next section shows a connection with the larger body. This is the first appearance of this group, but in the previous sections there is a circular space indicating where it has been but from which it has in some way been lost. There is a cleft entirely through the regular section, but this was where the cells had pulled apart and not where they had degenerated. The direct divisions are intimately associated with the necrotic spots. In the middle segment there are two indirect divisions on the edge

of the necrotic area, but usually they are near the free edge of the nest.

In the succeeding section the subnest has joined the limb of the main body and it was all counted together. There are three necrotic areas in this section. In the lower one the two directly dividing cells of that region are on the edge of the degenerated area.

A later section shows the nest in two segments, broken apart from each other. A pluripolar cell division shows at one place.

The group of cells drawn under high power in figure 15 is from this section. Figure 15 shows a group of five directly and one indirectly dividing cells. In this drawing and those made hereafter I shall indicate the segments of the nucleus as they appear through the depth of the cell, demonstrating their overlapping. The border line used was drawn at the edge of the cells which presented no marked degeneration changes, but it is not a hard, fast line, a few vigorous cells jutting out farther than the line and a few chromatic cells being behind it. Cells *A, B, C, D* and *E* show well-marked direct divisions. Cell *A* is on the necrotic border. Cell *B*, a very small cell for a directly dividing one, is a half cell width from the necrotic border. Cell *C* is a trifle closer than *B* to the border. Cell *D* is in the third row from the border. It is peculiar in that its chromatin nucleoli in each segment are not staining deeply and the chromatin is diffused through the karyoplasm. Cell *E* is in the fourth row from the necrotic edge. Cell *F* is an indirectly dividing cell and is in the same row of cells as cells *C* and *B*. Cells *G* and *G'* are the "chromatic cells" described under figure 13. They mark the edge of the necrotic plug and are in various stages of degeneration, as indicated by the disintegration of their cytoplasm and the loss of the staining power of their chromatin. This sketch together with the smaller one shows well this collecting of large numbers of the directly dividing cells about these necrotic areas. There are mitotic cells here, but not in such proportion in comparison to their total number as the amitotic.

FIGURE 16. In this section there are more direct divisions than indirect. There is a noticeable change in the number of indirect divisions in the lower part of the nest, in what was termed a "subnest" in a preceding section. In one section there are nine indirect divisions, two direct. In the next there

are eight indirect divisions, two direct. In the next there are five indirect divisions, three direct. In a later (fig. 16), there are five indirect divisions, four direct. In another (fig. 19), there are four indirect divisions, three direct. This shows consistently in this case that as the center of the nest is approached in the sections the number of direct divisions increase in proportion while the indirect decrease in proportion. In the region of the arrow point of figure 16 an enlarged drawing was made (figure 17). I used this to show more detail about the cells shown in figure 16. Cell *A* was on the edge of the necrotic area. Its chromatin was small in amount and gathered in two clumps in one segment and three in the other. Cell *C* is an ordinary dividing cell. Cell *D* is in the second row from the necrotic edge. The cross-hatched work shows the necrotic area, this area being entirely necrotic and showing no transition cells along the edge.

FIGURE 18. There are but two dividing cells in the upper segment of this nest, while in an earlier there are fourteen, the number decreasing with each section until this one. They have increased steadily in the middle part of the limb, however, from eleven to nearly twenty in the section shown in figure 18. This carefully worked out will demonstrate that at the same time the cells in one part of the nest are rapidly dividing those in another part are not dividing at all. There is either an unequal stimulus to growth in the nest or an unequal negative cause.

FIGURE 19. This nest is the same one as that in the preceding figure, but in this section the two parts have been separated. At the point of the arrow is the location of figure 20, and here are shown the three dividing cells drawn in figure 20. In figure 20, cell *A* is plainly among the degenerating cells in the necrotic plug, and is surrounded by "chromatic cells," no vigorous cell being near. It is a large clear cell with a bisegmented nucleus and showing but very little chromatin. Its appearance indicates that it is a degenerating cell. Cell *B* lies just outside the border of vigorous cells. Its nucleus is bisegmented and it stains much deeper than the cytoplasm. The chromatin nucleoli stain very faintly. Cell *C* is a large clear cell lying in the third row of cells from the necrotic edge. It stains lighter than the other cells about it and shows a small amount of chromatin and that stained faintly. Cells *A* and *B*

are noticeable because they have broken off from the vigorous growth and lie among cells that are distinctly necrotic.

Out of the 294 direct divisions in all the nests only 7 occurred in the first row on the edge of the nest.

Out of the 357 indirectly dividing cells 63 occurred in the first row on the edge of the nest.

The direct divisions in all the nests averaged 1.68 rows nearer the center than the indirect divisions.

CELL NEST 12. This nest was sketched and counted in forty-two serial sections. It began as three or four groups of cells which were the cross sections of limbs which later fused into a common trunk. It was non-necrotic throughout.

CELL NEST 12, I.

Tier	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*Av.*	*D.D.*	*I.D.*	*Cells*
Direct D.	.	.	1	.	.	.	.	3.0	1	..	...
Indirect D.	2	1	4	.	.	.	.	2.2	.	7	166

CELL NEST 12, II.

Direct D.	.	.	.	.	.	.	.	..	.	..	...
Indirect D.	.	4	.	1	1	.	.	2.8	.	6	140

CELL NEST 12, III.

Direct D.	.	2	.	.	.	.	.	2.0	2	..	...
Indirect D.	.	1	.	.	.	.	.	2.0	.	1	78

CELL NEST 12, IV.

Direct D.	.	.	1	.	.	.	.	3.0	1	..	...
Indirect D.	2	.	.	1	.	.	.	2.0	.	3	77

CELL NEST 12, V.

Direct D.	.	.	.	.	.	.	.	..	.	..	...
Indirect D.	2	3	1	.	.	.	.	1.8	.	6	180

CELL NEST 12, VI.

Direct D.	.	.	1	.	.	.	.	3.0	1	..	...
Indirect D.	.	1	1	.	.	.	.	2.5	.	2	81

CELL NEST 12, VII.

Direct D.	.	1	1	.	.	.	.	2.5	2	..	...
Indirect D.	.	.	2	1	.	.	.	2.3	.	4	85

CELL NEST 12, VIII.

Direct D.	.	.	.	.	.	.	.	..	.	..	...
Indirect D.	1	3	.	3	.	.	.	2.7	.	7	83

CELL NEST 12, IX.

Direct D.	.	.	1	1	.	.	.	3.5	2	..	...
Indirect D.	1	1	1	.	.	.	.	2.0	.	3	86

CELL NEST 12, X.

Direct D.	.	.	.	2	.	.	.	4.0	2	..	...
Indirect D.	2	2	.	.	.	.	.	1.4	.	4	169

Cell Nest 12, XI.

Direct D.	.	.	.	.	.	.	.	.	..	.	..	...
Indirect D.	3	3	2	.	.	.	.	.	1.9	.	8	206

Cell Nest 12, XII.

Direct D.	.	.	.	.	.	.	.	.	..	.	..	...
Indirect D.	2	2	2	.	.	.	.	.	2.0	.	6	227

Cell Nest 12, XIII.

Direct D.	1	1	.	.	3	.	.		3.6	5	..	...
Indirect D.	6	1	.	.	.	.	.		1.1	.	7	235

Cell Nest 12, XIV.

Direct D.	.	.	.	4	.	.	.		4.0	1	..	...
Indirect D.	5	.	2	.	.	.	.		1.5	.	7	360

Cell Nest 12, XV.

Direct D.	.	.	.	.	1	.	.		5.0	1	..	...
Indirect D.	3	.	2	.	1	1	.		2.8	.	7	328

Cell Nest 12, XVI.

Direct D.	.	.	.	1	.	.	.		4.0	1	..	...
Indirect D.	3	.	1	1	2	1	.		3.2	.	8	335

Cell Nest 12, XVII.

Direct D.	.	.	1	1	.	.	.		3.5	2	..	...
Indirect D.	4	2	1	1	.	.	.		1.9	.	8	365

Cell Nest 12, XVIII.

Direct D.	.	.	.	1	.	.	.		4.0	1	..	...
Indirect D.	9	.	2	.	1	.	.		1.6	.	12	362

Cell Nest 12, XIX.

Direct D.	.	.	.	.	1	1	.		5.5	2	..	...
Indirect D.	5	.	.	.	.	1	.		1.6	6	..	309

Cell Nest 12, XX.

Direct D.	.	.	1	.	.	1	.		4.5	2	..	...
Indirect D.	1	3	.	1	.	1	.		2.5	.	6	332

Cell Nest 12, XXI.

Direct D.	.	2	.	.	.	.	.		2.0	1	..	...
Indirect D.	2	1	.	.	.	.	.		1.3	.	3	215

Cell Nest 12, XXII.

Direct D.	.	.	.	.	.	.	.		..	.	..	...
Indirect D.	1	4	1	1	.	.	.		2.4	.	7	209

Cell Nest 12, XXIII.

Direct D.	1	1	.	1	1	.	.		3.0	4	..	...
Indirect D.	2	.	2	.	.	.	.		2.0	.	4	254

Cell Nest 12, XXIV.

Direct D.	.	1	.	.	.	.	.		2.0	1	..	...
Indirect D.	6	1	2	.	.	.	.		1.5	.	9	288

Cell Nest 12, XXV.

Direct D.	.	.	.	.	1	.	.		5.0	1	..	...
Indirect D.	2	3	.	.	.	.	.		1.7	.	5	449

Cell Nest 12, XXVI.

Direct D.	.	.	1	1	.	1	.	4.3	3	..	...
Indirect D.	5	4	.	.	.	.	.	1.4	.	9	316

Cell Nest 12, XXVII.

Direct D.	.	1	2	.	.	1	.	3.5	4	..	...
Indirect D.	6	3	2	.	.	.	.	1.6	.	11	230

Cell Nest 12, XXVIII.

Direct D.	.	1	1	2	.	.	.	3.2	4	..	...
Indirect D.	3	2	1	1	1	.	.	2.4	.	8	334

Cell Nest 12, XXIX.

Direct D.	.	1	.	.	.	.	.	2.0	1	..	...
Indirect D.	3	.	2	2	.	.	.	2.4	.	7	293

Cell Nest 12, XXX.

Direct D.	.	.	2	.	.	.	.	3.0	2	..	...
Indirect D.	5	2	1	.	.	.	.	1.5	.	8	307

Cell Nest 12, XXXI.

Direct D.	1	.	.	.	.	.	.	1.0	1	..	...
Indirect D.	3	2	1	.	.	.	.	1.6	.	6	334

Cell Nest 12, XXXII.

Direct D.	.	1	.	.	.	1	.	4.0	2	..	...
Indirect D.	1	2	1	.	.	.	.	2.0	.	4	281

Cell Nest 12, XXXIII.

Direct D.	1	.	.	.	1	1	.	4.0	3	..	...
Indirect D.	5	1	1	.	.	.	.	1.4	.	7	435

Cell Nest 12, XXXIV.

Direct D.	1	1	.	.	1	.	.	2.6	3	..	...
Indirect D.	2	.	1	.	1	.	.	2.5	.	4	381

Cell Nest 12, XXXV.

Direct D.	.	1	.	.	.	2	.	4.6	3	..	...
Indirect D.	5	2	.	.	1	.	.	1.7	.	8	431

Cell Nest 12, XXXVI.

Direct D.	.	.	.	.	1	1	.	5.5	2	..	...
Indirect D.	4	3	1	2	.	.	.	2.1	.	10	479

Cell Nest 12, XXXVII.

Direct D.	.	3	.	1	.	.	.	2.5	4	..	...
Indirect D.	3	6	1	1	.	.	.	2.0	.	11	537

Cell Nest 12, XXXVIII.

Direct D.	.	1	.	.	.	1	.	4.0	2	..	...
Indirect D.	6	2	1	1	.	.	.	1.7	.	10	551

Cell Nest 12, XXXIX.

Direct D.	1	.	.	3	.	1	1	4.3	6	..	...
Indirect D.	5	4	1	1	.	.	.	1.8	.	11	498

Cell Nest 12, XL.

Direct D.	.	.	.	.	2	.	.	5.0	2	..	...
Indirect D	6	2	2	.	.	.	.	1.6	.	10	410

CELL NEST 12, XLI.

Direct D.	.	2	.	.	.	.	.	2.0	2	..	...
Indirect D.	2	.	.	.	.	.	3	4.6	.	5	371

CELL NEST 12, XLII.

Direct D.	.	1	1	.	.	2	.	4.2	4	..	...
Indirect D.	4	2	3	.	.	1	.	2.3	.	10	421

No. of cells.	*Direct divisions.*	*Indirect divisions.*
12,228	81	285

Percentage of cells in divisions	2.99
" of cells in direct divisions	.6
" of cells in indirect divisions	2.3
" of divisions which are direct	22.1
" of divisions which are indirect	77.9

Table of all the nests counted, showing percentage of cells in division, percentage of cells in direct division, and percentage of cells in indirect division:

Cell nest.	*Percentage of cells in division.*	*Percentage of cells in direct division.*	*Percentage of cells in indirect division.*
2	4.42	1.5	2.9
3	4.34	1.9	2.4
4	3.88	2.3	1.5
5	3.77	0.0	3.77
6	2.36	1.7	.6
7	4.06	0.0	4.06
8	4.01	1.6	2.4
9	3.34	2.6	.7
10	3.39	1.5	1.8
11	3.59	1.9	1.6
12	2.99	.6	2.3

The writer of this paper wishes here to acknowledge his indebtedness to Doctor McClung, whose kind suggestions made this work possible, and to Doctor M. T. Sudler for the material and clinical data upon which this study is based.

CONCLUSIONS.

1. The percentage of cells in division shows no relation to the percentage of amitoses or mitoses.

2. The percentage of mitoses is high in small non-necrotic nests.

3. The percentage of amitoses is high in large necrotic nests, indicating that it is the division associated with degeneration.

4. Amitosis is the form of division occurring in the necrotic area.

5. The rate of division in the various nests is inconstant.

6. The directly dividing cells lie nearer the center of the cell

nests and thus nearer the necrotic areas than the indirectly dividing cells.

7. The indirectly dividing cells lie nearer the periphery of the nest than the directly dividing cells.

8. From these observations it may therefore reasonably be concluded that amitosis represents the final effort of the cell at reproduction, and that shortly after its occurrence degeneration ensues.

9. Amitosis, mitosis and disintegration comprise the cell changes in the alveoli.

10. Cells in direct and indirect division are larger than the resting cells.

11. In one stage of degeneration of the cells the chromatin becomes diffused through the karyoplasm and so swells that it fills the nucleus as a deeply staining, homogeneous mass. In another process of degeneration the chromatin loses its staining power and the cell becomes clear.

12. There is a shrinkage of the nuclear bulk in degeneration.

13. A border of chromatic cells lies between the vigorous cells and the cell debris of the necrotic area and marks the limit of degeneration; such cells are themselves degeneration results.

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CONTENTS:

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THE TEMNOSPONDYLOUS AMPHIBIA AND A NEW SPECIES OF *ERYOPS* FROM THE PERMIAN OF OKLAHOMA.

BY ROY L. MOODIE.

(Contribution from the Zoölogical Laboratory, No. 189.)

Plates XLIX to LIV.

OUR knowledge of the fossil Amphibia begins with Dr. J. J. Scheuczer's discovery of two skeletons in the Miocene of Oeningen, which he referred to as "*Homo diluvii testis et Theoskopos*," and which later Hermann von Meyer designated "*Andrias scheuczeri*," thus keeping the same idea in the generic name as Scheuczer had expressed in his letters and descriptions. The discovery was made about 1725, so far as I can ascertain. His letter to Sir Hans Sloane in 1726, which was translated in the republished volume of the early transactions of the Royal Society of London, is the first definite mention I find of this discovery in the literature which is accessible to me.

Exactly one hundred years elapsed from the time of Scheuczer's discovery of the giant salamander skeletons to the time when Dr. Georg Friedrick Jaeger discovered in the Triassic of Germany some labyrinthodont remains which he figured and described in his folio published in 1824 at Stuttgart with the title "De Ichthyosauri sive Proteosauri Fossilis Specimenibus in Agro Bollensi in Wurtembergia." He figured the occipital portion of the skull and teeth of what he, in 1828, called "Mastodonsaurus." In 1833 Doctor Jaeger pointed out the synonymy of *Salamandroides* with *Mastodonsaurus*. Previous to

Doctor Jaeger's discovery, however, was that of the form *Pygopterus*, the history of which is given below.

The literature on fossil Amphibia for the next twenty years following Jaeger's last mentioned paper deals almost entirely with the Tertiary Amphibia, although in 1844 and 1845 Hermann von Meyer published some interesting papers on the more ancient amphibians. It is interesting to note that in von Meyer's "System der fossilen Saurier," 1845, he does not mention a single temnospondylous amphibian.

Our knowledge of the Temnospondylia dates from the year 1847, in which year Dr. August Goldfuss described *Archegosaurus*, the first known and for many years the only representative of this order of amphibians. Doctor Goldfuss gave as the title of the paper in which he described *Archegosaurus* "Ueber das ælteste der mit Bestimmtheit erkannten Reptilien." It will thus be noticed from the literature that the early writers regarded the labyrinthodonts and their allies as reptiles. It was Quenstedt who in 1850 made the first contention that "Die Mastodonsaurier im gruenen Keuper Sandstein Wurtemburgs sind Batrachier," and from that time dates the development of our knowledge of these extinct forms as Amphibia. Three years after Quenstedt's paper appeared, Vogt upheld the same contention in his essay "Archegosaurus und all Labyrinthodonten sind Amphibien nicht Reptilien."

In 1850, after the discovery of the *Archegosaurus* and its identification, Doctor Jaeger published an interesting essay entitled "Ueber die Uebereinstimmung des *Pygopterus lucius* Ag. mit dem *Archegosaurus dechenii* Goldf." In this essay Jaeger brings out the interesting facts of the early discovery of the *Archegosaurus*. I give the following translation of the first paragraph of Jaeger's essay: "In the collection of the late Professor Storr, of Tübingen, which was received in 1817 at the Imperial Museum of Natural History at Stuttgart, there was found a skull enclosed in a spherosiderite nodule. This skull was listed in 1777 as No. 192, in the printed catalogue of the Pasquay collection (which was the foundation of the Storr collection), without giving the locality, as a fish skull which had been discovered in a non-fissile gray shale. Agassiz, at whose disposal the entire collection of fossil fishes was soon after placed, designated this specimen on a label in his own handwriting at first as *Aspidorhynchus* nov. sp. On a label written

by him later it is designated as *Pygopterus lucius*. In the first part of the second volume of the Fossil Fishes (Poissons fossiles), page 10, Agassiz placed this skull in the family Sauroidæ as the second species of the genus *Pygopterus*, with the short description: '*Pygopterus lucius* Ag., une tête seulement, dont la mâchoire supérieure est plus allongée. Houille de Saarbrück.' In the same work, part II, page 78, this specimen is designated as the fifth species of *Pygopterus*, with the description, 'une tête avec des dents très acerées, de la houille de Saarbrück. L'original se trouve au Musée de Stuttgart.' He regards the same specimen as the third species on page 162 in the synoptic table of the family Sauroidæ arranged in the order of the formations of the Carboniferous which contained Sauroidæ. It is also given this place in the general table of fossil fishes which appeared in 1844, page xxxvi."

Jaeger affirmed the supposition of Agassiz that the specimen was from Saarbrück, from the similarity of the nodule to those found at that place. He then proceeded to show that the skull described by Agassiz as *Pygopterus lucius* really shows reptilian characters which Jaeger regarded as intermediate between those of a crocodile and an *Iguana*. He then compared it with the skull of a young crocodile and also with the skulls of various lizards. He found that the measurements and proportions of the skull compare favorably with those of the crocodile, and that the teeth have the form and size of those of a newly born crocodile. The position of the orbit is also identical with that of the crocodile. He made the important observation that the nostrils have the lateral position of the lizards. He then compared the specimen with other known fossil forms, *i. e.*, *Zygosaurus, Rhinosaurus* and the labyrinthodonts, and found considerable differences. He then made the following interesting observations regarding *Archegosaurus:* "At the meeting of naturalists in Aachen in 1847 Goldfuss described the remains in one of the many spherosiderite nodules, which contained a reptile skull, to which he gave the name *Archegosaurus*. He established three species for the genus, which he described more fully in a later publication. Only one species of this genus, *Archegosaurus decheni*, was described and figured in the Neues Jahrbuch für Mineralogie, 1847, Tab. VI, with a line drawing." Jaeger then pointed out in a conclusive manner the identity of *Pygopterus lucius* with *Archegosaurus*. He re-

garded *Archegosaurus* as allied to the Crocodilia but having characters of the Batrachia as were exhibited in the labyrinthodonts, and on account of the geological position of the fossils he supposed that *Archegosaurus* would really belong with the labyrinthodonts.

Huxley in 1862 described *Pholidogaster pisciformis* from the Carboniferous of Scotland. In the next year he distributed the ancient Amphibia into the two groups, the Archegosauria and the Mastodonsauria of von Meyer. In the former group he placed *Pholidogaster*, to which it manifestly does not belong. Huxley was himself doubtful as to its location, for he says: "*Archegosaurus*, of course, takes its place among the Archegosauria; and *Pholidogaster*, I suspect, must go with it, though its vertebræ are far better ossified"; and in a footnote he makes the interesting statement: "It seems to me probable that the vertebral centra of *Archegosaurus* may really have been osseous rings, such as are found in embryo frogs and salamanders," which shows that he was on the right track but did not quite comprehend the nature of the vertebræ of *Archegosaurus*.

Our knowledge for the next few years of our history is advanced but little, and that only by sundry discussions on *Archegosaurus*. In 1866 Owen placed *Archegosaurus* in his subclass "Dipnoa," under the order "Ganocephala." In the same year Haekel retained Owen's classification, except that he displaced Owen's "Dipnoa" with "Phractamphibia." Cope, in 1868, retained essentially the same classification as proposed by Owen. In 1874 the committee of the British Association for the Advancement of Science reported on the extinct Amphibia, and placed *Archegosaurus* by itself in group VI, the Archegosauria.

No further additions were made to our knowledge of the Temnospondylia until 1875 and 1878, when Cope described *Cricotus* from the Carboniferous of Illinois and *Trimerorhachis* from the Permian of Texas. In the next year Gaudry described *Actinodon* from the Permian of France. In 1882 a decided advance was made in the separation by Professor Cope of the rhachitomous forms such as *Eryops, Actinodon, Zatrachys, Trimerorhachis* and other genera, which have subsequently proven to be synonyms of the genera mentioned, into a distinct group. Cope proposed the term Rhachitomi for this subordinal group, and designated two families, the Eryopidæ and the Trimeror-

hachidæ as its members. Later in the same year Cope described *Acheloma* from Texas. In 1885 Lydekker added other genera and families to the group, notably *Gondwanosaurus*, which he placed in the family Archegosauridæ. In 1884 Cope, and in the following year Fritsch, contributed further to the knowledge of the Temnospondylia by the description of the forms *Diplospondylus* and *Cricotus* from the Permian of Bohemia and Texas. In 1888 Zittel proposed to place all temnospondylus amphibians under the suborder Temnospondyli in two groups—A, those with rhachitomous vertebræ; B, those with embolomerous vertebræ—for which two groups Cope had previously, 1885, proposed the terms Rhachitomi and Embolomeri, but had regarded them as coördinate with the group Stegocephali.

Case, Broili, and others have in recent years given additional information on the forms previously described and have described some new forms. In 1909 Dr. S. W. Williston, in his essay on "*Trematops milleri* from the Permian of Texas," was enabled to give a restoration of the skeleton of that form. In the present bulletin the writer will describe an interesting new embolomerous amphibian under the name *Spondylerpeton spinatum*, from the Coal Measures of Mazon Creek, Illinois. This is the oldest of the known Temnospondylia.

We know nothing of the ancestry of the Temnospondylia. They occur in the Carboniferous and Permian, and if the Stereospondylia are highly specialized Temnospondylia, as seems probable, they also occur in the Triassic, but this is yet to be proven.

The geographical distribution of the Temnospondylia is as follows: In the Carboniferous and Permian of North America; Europe; and Asia, in the Permocarboniferous of India, *Gondwanosaurus*. So far as the writer is aware they occur nowhere else unless some of the little known forms from South Africa will, on further search, reveal temnospondylous characters. It is entirely too soon to arrive at any conclusions as to the paths of migration of this group. They followed the way which was open to other land animals, whatever that may have been.

Nor can we say in what region the first of the Temnospondylia lived. Judging from the remains so far discovered their place of origin must be located in North America. The announcement of the discovery of the eryopoid form from Pitts-

burg, Pa., by Case, and the discovery by the writer of the cricotoid form in the Mazon Creek fauna, as well as the presence of Carboniferous Cricotidæ in Illinois and Kansas, all point to an origin of the temnospondylous group at an earlier date in North America than in any other region of the globe. The embolomerous forms are by far the older.

The species of fossil Amphibia from the Carboniferous, Permian and Triassic are so little known that it is difficult to give a definite list of the species of the Temnospondylia. The list given below is believed to be approximately accurate. It does not differ in essential outlines from that given by Zittel in 1887. The species are distributed in the various groups to which, at the present time, they seem to belong:

CLASS—AMPHIBIA, Linné, 1758.

Order—Temnospondylia, Zittel, 1887.
Suborder—Rhachitomi, Cope, 1885.

Family—Eryopidæ Cope, 1882.

Eryops megacephalus Cope, 1877. Permian of Texas.
" erythrolithicus Cope, 1878. Permian of Texas.
" ferricolus Cope, 1878. Permian of Texas.
" reticulatus Cope, 1881. Permian of Texas.
" ? platypus Cope, 1877. Carboniferous of Ohio.
" latus Case, 1905. Permian of Texas.
" willistoni Moodie, 1911. Permian of Oklahoma.
Trematops milleri Williston, 1909. Permian of Texas.
Acheloma cumminsi Cope, 1882. Permian of Texas.
Ichthycanthus ohiensis Cope, 1877. Carboniferous of Ohio.
Gondwanosaurus bijoriensis Lydekker. Bijori, India.
Zatrachys apicalis Cope, 1881. Permian of Texas.
" conchigerus Cope, 1896. Permian of Texas.
" crucifer Case, 1905. Permian of Texas.
" micropthalmus Cope, 1896. Permian of Texas.
" serratus Cope, 1878. Permian of Texas.
Actinodon frossardi Gaudry, 1880. Permian of France.
" latirostris Jordan. Permian of France.
* (?) Anisodexis enchodus Cope, 1897. Carboniferous of Ohio.
* " imbrecarius Cope, 1882, Permian of Texas.
*Rhytidosteus capensis Owen, 1884. Karoo Beds, South Africa.
(?) *Euchirosaurus rochei Gaudry. Permian of France.

Family—Trimerorhachidæ Cope, 1882.

Trimerorhachis bilobatus Cope, 1883. Permian of Texas.
" conangulus Cope, 1896. Permian of Texas.
" insignis Cope, 1878. Permian of Texas.
" mesops Cope, 1896. Permian of Texas.
" leptorhynchus Case, 1902. Permian of Oklahoma.
Cricotillus brachydens Case. Permian of Oklahoma.
Archegosaurus austricus Makowsky, 1876.
" decheni Goldfuss, 1847. Permian of Germany.
" latifrons Gein. & Deich. Permian of Saxony.
" ornatus Woodward, 1905. Permian of India.

Platypodosaurus ricardi Twelvetrees, 1880. Permian of Russia.
" stückenbergi Trautschold. Zechstein of Russia.
Cochleosaurus bohemicus Fritsch, 1876. Permian of Bohemia.
Gaudrya latistoma Fritsch, 1885. Permian of Bohemia.
Chelyosaurus vranyi Fritsch, 1878. Permian of Bohemia.
*Sphenosaurus sternbergi Fitzinger, 1840. Permian of Bohemia.
Sparagmites lacertinus Fritsch, 1885. Permian of Bohemia.
*Sclerocephalus hauseri Goldfuss. Permian of Germany.
*Sclerocephalus credneri Fritsch. Permian of Bohemia.
*Sclerosaurus bavaricus Branco. Rothl. Ohmbach.
*Melosaurus uralensis H. von Meyer. Kupfersandstein.
*Osteophorus roemeri H. von Meyer. Rothl. Schliessen.
*Zygosaurus lucius Eichwald. Permian of Russia.

Gonioglyptus huxleyi Lydekker from the Gondwana beds of India also possibly belongs in this family.

So many genera and species of extinct Amphibia are based on fragments of crania or limbs that an exact diagnosis of the forms is impossible. The species marked with a star (*) are uncertain as to position. Many of the species listed under the Trimerorhachidæ are placed in this family on the authority of Lydekker, who included them in his family Archegosauridæ, which was preoccupied by Trimerorhachidæ. Doctor Williston regards *Trematops milleri* Will. and *Acheloma cumminsi* Cope as representatives of a family distinct from the Eryopidæ for which in 1910 he proposed the name Trematopsidæ. He also regards the species of *Zatrachys* as entitled to family rank in the Zatrachydidæ, Williston, 1910.

Euchirosaurus of Gaudry is probably a reptile.

Suborder—EMBOLOMERI, Cope, 1881.

FAMILY—CRICOTIDÆ Cope, 1884.

Cricotus gibsoni Cope, 1877. Carboniferous of Illinois.
" crassidiscus Cope, 1884. Permian of Texas.
" heteroclitus Cope, 1875. Carboniferous of Illinois.
" hypantricus Cope, 1884. Permian of Texas.
" sp. indet. Case. Carboniferous of Illinois.
Diplospondylus punctatum Fritsch. Permian of Bohemia.
Spondylerpeton spinatum Moodie, 1910. Carboniferous of Illinois.
? *Discosaurus permianus Credner. Permian of Saxony.

FAMILY—DISSOROPHIDÆ Williston, 1910.

Dissorophus multicinctus Cope, 1895. Permian of Texas.
" mimeticus Cope, 1896. Permian of Texas.
" testudineus Cope, 1896. Permian of Texas.
Cacops aspidephorus Will. 1910. Permian of Texas.
Aspidosaurus chiton Broili, 1904. Permian of Texas.

From the foregoing diagnosis is will be seen that about 55 species of the 350 which have been assigned to the fossil Amphibia of the world can be located in the order Temno-

spondylia. Without doubt some of these species will prove invalid and there will be others already described which will in time prove to belong to this group, but the above statements represent an approximation of our present knowledge.

Since the present essay is to deal especially with a new member of the genus *Eryops,* only those groups will be here defined to which *Eryops* and its allies pertain.

ORDER—TEMNOSPONDYLIA, Zittel, 1887.

Terrestrial or semiaquatic vertebrata; skull bones pitted and grooved; lateral line canals present; pineal foramen sometimes absent; sclerotic plates present; vertebræ rachitomous or embolomerous; notochord usually persistent; one or two sacral vertebra; tail present, short or long; limbs and girdles all well developed; pectoral and pelvic girdles composed of the usual stegocephalan elements; an osseous pubis present; cleithrum present on the scapula in some forms; limb bones well developed and bones of forearm and leg separate; carpus and tarsus osseous, 12 elements present in tarsus of one form, 11 carpals; five digits in hand and foot; phalangeal formula 2, 3, 3, 4, 2 (?) for the hand and 2-3-3-3-2(?) for the foot; venter covered with an armature of osseous scutes, sometimes overlapping; skin of back bare or armored; ribs heavy, double-headed, curved, and either moderately long or short. Body short and heavy. As compared to skull, about two to one. Temporal foramina present in a few forms.

Range. Pennsylvanian to (Triassic) Upper Permian.

Distribution. North America—Illinois, Kansas, Oklahoma and Texas. Europe—Germany, Bohemia, France. Asia—India.

The suborder Rhachitomi is characterized solely by the nature of the vertebral column, which is cut into triangular segments.

FAMILY—ERYOPIDÆ Cope, 1882.

Large terrestrial or amphibious vertebrata; skull bones deeply marked with pits and grooves which at times take the form of lateral line canals; carpus and tarsus osseous; pubis osseous; pentadactyl fore and hind limbs; orbits in the typical genus located far back on the skull and near the median line; cleithrum present on the scapula; vertebræ rachitomous, the intercentrum supporting the arch in the dorsal region; para-

sphenoid well developed or reduced; teeth on pterygoids, palatines, prevomers and parasphenoid.

Range. Upper Pennsylvanian to Permian.

Distribution. America, Europe, Asia.

Genus—Eryops Cope, 1877.

The following definition of the genus is given by Doctor Branson: "Skull long, comparatively narrow; proportion of length to breadth about nine to seven. Roof bones coarsely sculptured posteriorly, finely sculptured anteriorly. Nasals and premaxillæ very large; frontals excluded from orbits by junction of pre- and post-frontals. Pterygoids not meeting in the median line; parasphenoid dagger-shaped, tapering gradually to a point just in front of the palatine foramina; prevomers large. Orbits subcircular, situated in the posterior half of the skull; nares subovate, remote, at a considerable distance from the tip of the skull. Many minute denticles on pterygoids, palatines, prevomers and parasphenoid. Teeth circular in cross section, strongly ribbed near base, dentine strongly infolded. Three large teeth on each palatine. Mandible without postcotyloid process. Vertebræ rachitomous. Ribs double-headed. Pelvic bones coalesced."

There have been up to the present five species of *Eryops* described, with a doubtful sixth, ? *Eryops platypus* Cope, from the Carboniferous of Ohio.

In 1889 Lydekker described a species of *Eryops, E. africanus,* from the Karoo beds of South Africa. Broom has subsequently shown that this species does not belong in this genus and has placed that species with two others in his genus *Rhinesuchus,* in which he includes *R. (Macromerion) gumbeli* (v. Ammon), *R. (Eryops) africanus* (Lydekker), and *R. whaitsi* Broom.

An additional species of *Eryops* is represented by remains in the collection of the University of Kansas and it is here described as new.

Eryops willistoni, new species.

Dr. S. W. Williston in 1899 described and partially figured in the *Kansas University Quarterly* portions of a skeleton of a species of *Eryops,* which he tentatively referred to the species *Eryops megacephalus* Cope. He has several times expressed to me the opinion that the form is distinct from *E. megacephalus,* and a recent careful study of the ma-

terial has led me to regard the remains as a new species, which may be very appropriately named *Eryops willistoni* as a partial expression of gratitude to my honored preceptor in paleontology. Since, also, several interesting points in anatomy and morphology have come up for consideration the following discussion is presented in the hope of adding some knowledge on this peculiar Permian genus.

The material which represents the present species comprises the following portions of the skeleton: Portions of the skull; several teeth and a nearly entire right mandible; the scapula-coracoid of both sides, incomplete; the right clavicle; portion of the interclavicle; right humerus, radius, ulna and a phalange; about a dozen vertebræ and the left sacral rib.

There are various fragments of the skull preserved. On one of these fragments is observed a portion of the right orbit and a part of the prefontal and frontal bones clearly marked off by sutures. The present form differs in this respect from the known specimens of *Eryops megacephalus*, in which the sutures remained unknown until they were discovered by Doctor Branson, who was able to trace them with the aid of a lens. On the present specimen the sutures stand out with almost startling distinctness. They do not have the sharply zigzag form assumed in *E. megacephalus* and other of the larger Amphibia, but the sutures occur in bold curves. I detect a portion of the supraorbital lateral line canal on the fragment containing the orbit. The sculpture of the cranial bones in the present form is quite different from that of *E. megacephalus*. It is much more rugose and the rugosities have a larger form. This holds true for the mandible also (plate XLIX, fig. 1), and it is taken as one of the specific characters.

There are preserved in the collection also a single complete tooth and fragments of others. The complete tooth (plate XLIX, fig. 2) is of the typical labyrinthodont form. It is oval in cross section with sides flattened. It arises from a tumid base of cancellated bone as in the mosasaurs. It is recurved and sharply pointed.

In 1899 Ludwig Strickler (Paleontographica Bd. XLVI, p. 85, plates XI, XII) investigated the minute structure of the teeth of *Eryops megacephalus*.

The mandible of the present species is preserved in a much broken condition, but its form is nearly complete. The form and ornamentation of the posterior portion were well shown in

Williston's figure (Kan. Univ. Quart., Ser. A, vol. VIII, pl. XXX, fig. 1), which is reproduced here with slight changes. The sharp angulation and the posterior position of the angle is a specific character which serves to distinguish this species from *Eryops megacephalus* Cope, to which the present form is most nearly allied.

The jaw (plate XLIX, fig. 1), is heavy and elongate. The portion posterior to the coronoid angle is an acute triangle which ends in the articular. Only a portion of the suture bounding the articular can be distinguished. This is indicated in the figure. The coronoid suture is evident for its entire course. The suture starts from the articular suture, and running directly forwards turns upward just before reaching the teeth, which do not occur on the coronoid. This element is a thin bone superiorly but more thickened below. The sutures separating the angular, surangular and dentary cannot be determined. The angular and surangular contain, on their external surface, the peculiar nodose ornamentations which help to characterize the present species.

The sculpture on these elements consists of scrobiculate knobs some 5 to 7 mm. in diameter. This ornamentation ends apparently at the dentary, since the tooth-bearing element, which is quite large, is ornamented only with coarse elevations and pits.

The operculo-mandibular lateral line canal can be traced as a depression beginning on the articular and running forward as far as the bone is clearly preserved. It occurs as a shallow groove interrupted by the nodose and scrobiculate sculpturing of the mandibular elements. The internal surface of the mandible is not preserved in sufficient detail for description.

Complete teeth are lacking from the mandible in its present condition. Doctor Williston figured two of them as complete, and it is quite probable that they have been broken off since he studied the specimen, because the material is excessively fragile. The hollow character holds for all of the tooth bases which are preserved on the mandible. An additional portion of the mandible is shown in figure 5, plate XLIX. Its characters do not differ from those described above.

In regard to the hollow nature of the teeth, Tomes has the following explanation: "The laminæ of pulp, with their several systems of dentinal tubes, instead of passing out in straight

lines like the spokes of a wheel, pursue a tortuous course as they run from the central small pulp chamber toward the surface. Not only do they undulate, but they give off lateral processes, and at their terminations near the surface of the tooth the thin laminæ of pulp (so thin that the radiating pulp chambers are mere fissures) become dilated; so that on section circular canals are seen at these points, as is also the case at the points where subsidiary processes branch off." (Dental Anatomy, 5th edition, 1898, p. 65.)

Measurements of the mandible of *Eryops willistoni:*

Greatest length	48 cm.
Length of posterior portion (fig. 1)	33
Greatest width	10
Width of dentary midway from coronoid process	6.5
Width across articular	2.6
Length of tooth	2.
Thickness of same at base	.5

The right arm of this species is preserved in an incomplete condition, as may be seen by reference to plate LII. The form of the humerus is well shown in the figures, plate LIII, fig. 7, and plate LII. It suggests to a certain extent the humerus of a mosasaur. The present element does not have the bizarre appearance which exists with the specimen of that element of *Eryops megacephalus* figured by Professor Cope in 1890 (Trans. Amer. Philos. Soc., vol. XVI, p. 367, fig. 3). The large projections are wanting entirely from one side and on the other they are not so highly developed, and yet the form of the bone is such that it can be nothing else save a humerus. It is too rugged for a femur.

The specimen is abraded to some extent, so that the exact form of the element cannot be determined. It may have had the form suggested by the broken lines in the figures. The humerus is that of the right side. Viewed from in front the element is seen to have a peculiar form (plate LIII, fig. 7). The lower portion of the inner surface is distinctly concave. The inner side of the bone is comparatively smooth. There is a low ridge which runs obliquely across the antero-superior angle of the bone. There is a distinct twist in the inner surface, which is continued to such an extent that the inner surface is carried around almost parallel with a portion of the outer surface. It then takes another and inward curve and ends in a projection.

One of the projections from the outer surface of the humerus

is in the form of a hook and strongly suggests the hooklike process which is developed in the quadrate of the mosasaurs. This hook and the other elevations on the edge of the bone without doubt served as points of attachment of the deltoid and pectoralis muscles, which were undoubtedly well developed in the species of *Eryops*.

The outer surface of the bone is exceedingly rough and there are no less than six distinct elevations on this surface. One of these elevations is a ridge which runs at somewhat of an angle across the posterior edge. There is an indication of a foramen opposite the pit which occurs on one side of the bone, which at first was thought to represent the entepicondylar foramen. This was such an important matter that the bone was cut through at this point by Mr. Martin and fully demonstrated the total absence of this foramen in the element although there is quite a distinct pit at this point. Cope described such a foramen in *Acheloma*, but Case, who has recently examined the type, says the foramen is an accidental opening. Gaudry likewise described such an opening in *Actinodon*.

Measurements of the humerus:

Length of specimen as preserved	96	mm.
Estimated length along same line	110	
Width at middle of shaft	50	
Width of top of humerus	90	
Width at lower end	72	
Thickness of head as preserved	23	
Diameter of entepicondylar pit	3	

The element which is here regarded as a radius is very similar in form to that described by Cope for *Eryops megacephalus*. Its form is well shown in the figure. The lower end is somewhat larger than the upper, which is abraded and broken. Viewed from the lower surface a cross section of the bone shows a semicircular form. It is hour-glass shaped in its entire length, with a shallow groove near the lower end. Both ends of the bone near the articular surfaces are roughened by vascular pits for muscular attachment or for the union of the cartilaginous tips.

Measurement of radius:

Actual length of specimen	91	mm.
Estimated length of specimen	95	
Width of upper end (estimated)	40	
Width at middle of shaft	24	
Width at lower end	60	
Thickness of base	32	

The element here figured as an ulna (plate LII, *U*) is doubtfully referred to the arm, since the bones were found disassociated. It may belong to the leg. Its form is specifically different from that which Cope figured as the ulna of *Eryops megacephalus,* although its form is, in general, the same. It does not depart widely, in point of form, from that of the radius, which we should expect to be the case in a generalized vertebrate. It is smaller, somewhat shorter, and the groove on the ventral (?) surface is lacking. The radius and ulna are both peculiarly amphibian in the way they have weathered. The ends have assumed the concave form so characteristic of the Branchiosauria and the modern Amphibia, indicating a higher development of the perichondrium than of the endochondrium.

Measurements of the ulna:

Actual length of specimen	80 mm.
Estimated length of specimen	93
Width of shaft at middle	22
Width of upper end (estimated)	47
Width of lower end (estimated)	40

Associated with the limb bones there is a portion of a phalange of the hand (?) of the specimen. There are no carpals preserved. The element figured (plate LIII, figs. 4 and 5) is probably a metacarpal. Its form is very closely similar to that figured by Cope for the metacarpal element of *Eryops megacephalus.* Its upper end is very broad, with recurving edges and with rugosities for muscular attachment. Its form is crescent shaped and concave. The shaft narrows abruptly from the upper end to the middle and then widens for the lower end, which is lost.

Measurements of the metacarpal:

Actual length of specimen	23 mm.
Estimated length of bone	27
Width of upper end	22
Thickness of upper end	8

The following description of the coraco-scapula (plates L, LI) is taken from Doctor Williston's paper. The description of the cleithrum is appended:

"The bone is elongated, and nowhere very thick or massive. The distal part of the scapula is much thinned and considerably expanded; the immediate margin here, however, is wanting, so that the precise outlines cannot be given.

"The position of the two bones must have been very oblique, as is evident from the position of the glenoid cavity. The pos-

tero-inferior border is moderately thickened, and rounded; gently concave along the proximal part and convex distally. The antero-superior border is much thinner than the opposite one, and is concave throughout the extent of the shaft, except distally, where it is coössified with the procoracoid. The union of these two bones is very close in this region, the sutural line being distinguished with difficulty if at all. The procoracoid is narrower and more thickened below, reaching to the lower part of the conjoined bone, and lying in close apposition though not suturally united. Both the lateral surfaces of the scapula are nearly flat. A little proximad to the narrowest part of the shaft the bone is much thickened by a stout ridge on the inner side, which includes between it and the remainder of the bone, just back of or above the cotylus, a large, elongated foramen, both of whose orifices can be seen from the inner side of the bone only.

"The glenoid surface is elongated and deeply concave in its long diameter. The scapular portion is much smaller than the coracoid, and is partly separated from it by a constriction; this surface is nearly flat and is placed at right angles to the plane of the coracoid surface, looking directly downward when the bone is lying horizontally. The rest of the cotylus is moderately concave and looks outward and somewhat backward and upward with the bone in its former position. Just how much of the conjoined bone is formed of each element it is impossible to say since the union is so close that no trace of a junction is perceptible. Evidently, however, the coracoid forms only a small part of the whole bone. Its anterior or inferior border is gently convex, the posterior one slightly concave.

"The anterior end of the superior border of the scapula is gently convex, as is also the broad external surface. On the inner side the foramen described above opens into a deep, elongated, boat-shaped cavity at its distal end, the cavity formed by the upper border of the ridge described. In the lower or anterior end of the cavity there are apparently two smaller foramina, the external orifices of which are just within the anterior margin of the scapular face of the glenoid surface. The proximal surface of the scapula is concave; that of the coracoid, if the bone is limited by the ridge spoken of, is for the most part gently convex and lies in a more mesial plane."

The scapula is evidently that of the right side, the same as the humerus described below.

On the antero-superior corner of the scapula is a part of a peculiar element—the cleithrum. Its occurrence in the genus *Eryops* has been noted by Case in two species. In *E. latus* the cleithrum takes a most peculiar form. The form assumed by the element in the present species is impossible to determine, since the greater part of it has weathered away.

The cleithrum is, apparently, simply laid on the upper edge of the scapula, the union being hardly a sutural one. In the present specimen it is represented only by the lower part, but it could not have had the immense expanse superiorly as Case and Williston have figured for the cleithrum in *Eryops latus* Case. It was probably quite slender, as it is in the dicynodont reptiles. The cleithrum is a thin plate of bone with a ridge running along the interior border. The edge of the scapula is depressed to receive the element.

The characters of the scapula which are at variance with the scapulæ of the known species are the narrowness of the shaft, the location and size of the cleithrum, and the position of the cotylus.

In regard to the three foramina seen and described in the scapula Williston has recently proposed the terms supra-, post- and infra-glenoid or supra-coracoid to designate these openings. The foramina occur in all known Temnospondylia, as well as in the Cotylosauria (2) and in the Pelycosauria (2). The writer has recently described a branchiosaurian from the Pennsylvanian of Mazon Creek in which three foramina are visible in the scapula. This was thought to be of interest in connection with the Temnospondylia, but investigation showed that in the temnospondyles the foramina are in no case to be regarded as occurring strictly in the scapula, but rather as belonging to the coracoid which is united with the scapula.

An interesting question of homologies, or it may be parallel development, arises in comparing the present scapula-coracoid with the clavicular apparatus of *Portheus*.

Measurements of scapula-coracoid:

Actual length of specimen	33.7 cm.
Estimated length of element	36
Width of upper end of scapula	15.5
Thickness at upper end	3 mm.
Width at middle of shaft	6.6 cm.
Width across coracoid portion	17

Length of cotylus	7.2	
Width of cotylus	3.8	
Diameter of infraglenoid foramen	5	mm.
Thickness of bone at lower edge	7	
Thickness of bone through cotylus	4.3	cm.
Length of portion of cleithrum preserved	63	mm.
Greatest width of cleithrum	22	

The clavicle of the right side is preserved almost completely (plate LIII, figs. 1 and 2). The element was figured by Doctor Williston but not described. It is strongly curved and spatulate. Its outer surface is ornamented with longitudinal grooves, which arise near the center of the bone and run each way, thus indicating its ossific center. The inner surface of the bone is smooth excepting for two vascular pits near the center. A prominent ridge runs along the dorsal inner edge of the bone.

Measurements of the clavicle:

Length along curve	24.7	cm.
Length across arc	20	
Least width	1.3	
Greatest width	4.6	
Greatest thickness	1	
Least thickness	2	mm.

There is a fragment of what I regard as the posterior projection of the interclavicle. If it is such it is either a pathological specimen or there were two projections from the posterior edge of the interclavicle, for the fragment is highly asymmetric. The spine, for such it is, has an irregular nodose surface as if for the attachment of cartilage. It is long, slender and somewhat flattened. (Plate LIII, fig. 3.)

Measurements of spine of interclavicle:

Length of specimen	13.7	cm.
Greatest width	2.2	
Least width	.75	

There are remains of about a dozen vertebræ preserved. Portions of three of these are figured in plate LIV, figures 1 and 2. They all have the characteristic rachitomous form assumed by the other species of *Eryops*. The divisions between the pleurocentra, hypocentra and neurocentra are well marked. The zygapophyses are well formed. The upper part of the neural spines is much thickened, as is the case often in specimens of *Eryops megacephalus* Cope. According to Broili the spines may also be bifurcate, as Cope has described for *E. erythrolithicus*. The enlarged spine was undoubtedly for the attachment of muscles to sustain the enormous head, and

spines showing different characters might very easily occur in various portions of the vertebral column.

Measurements of vertebræ:

Length of centrum	2.5 cm.
Width of centrum	3.2
Height of vertebræ to tip of spine	13.4
Thickness of top of spine	3

Broili (Monatsb. d. Deutsch, Geol. Gesell., Bd. 60, Texttafel p. 236, fig. 2) has figured in *Eryops megacephalus* a peculiar element which he has identified as the sacral rib, having found it in place with a sacral vertebra. There is no doubt that the present element (plate LIV, figs. 3 and 4) is the same as he has figured. Its interpretation as a sacral rib is somewhat surprising on account of the extreme thinness of the bone. It thins out to less than a millimeter on one edge. Its location any other place in the skeleton is, however, doubtful.

The element has a broad base as if for attachment suturally with the vertebral transverse process. The base of the specimen has been broken transversely and only a portion of the suture remains. The bone is flat immediately from the base and is greatly expanded and thinned distally. It is, for the most part, smooth, though there is a small roughened place on the dorsal (?) surface. The ventral (?) surface is marked by a depression which runs the entire length of the bone. The distal end is lost.

Measurements of sacral rib:

Actual length of specimen	90 mm.
Width at distal end	62
Width at middle of blade	32
Width at inner end	55

Eryops willistoni differs from *E. ferricolus* Cope in the absence of a raised rim to the orbits. From *E. erythrolithicus* Cope it differs in the non-bifurcation of the neural spines. This last is not a well-known species and may be synonymous with *E. megacephalus*. *E. reticulatus* is a small species, from which *E. willistoni* differs in the character of the cranial sculpture. It is distinct from *E. latus* Case on account of the dimensions of the scapula and the cleithrum. *E. megacephalus* also shows characters which are divergent from those of the present species. These are the shape and structure of the mandible and its ornamentation, the form of the humerus and

the shape and structure of the scapula-coracoid, as well as other structures which are characteristic.

The material on which the species *Eryops willistoni* is based is from the Permian of Oklahoma. It was collected by Prof. C. N. Gould in 1896, in the red sandstone southwest of Blackwell, Okla. The specimen is No. 348 of the Kansas University Museum.

I am indebted to Mr. G. Dallas Hanna for all of the drawings illustrating the present essay, except that on plate XLIX figure 1, which is from the pen of Mr. Sydney Prentice, at present with the Carnegie Museum.

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CONTENTS:

AN ARMORED DINOSAUR FROM THE UPPER CRETACEOUS OF WYOMING,
Roy L. Moodie.

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AN ARMORED DINOSAUR FROM THE CRETACEOUS OF WYOMING.

BY ROY L. MOODIE.

(Contribution from the Zoölogical Laboratory, No. 190.)

Plates LV to LIX, and one text figure.

IN *Science* for October 20, 1905, Dr. S. W. Williston (*1*) published a brief account of a remarkable armored dinosaur from the upper Cretaceous of Wyoming. He likewise gave a short sketch of the horizon from which the specimen was obtained, naming the horizon Hailey shales, and suggesting the name *Stegopelta landerensis* for the dinosaur.

During the summer of 1906, while searching these beds for plesiosaur remains for the Carnegie Museum (*2*) the writer followed the horizon eastward and northward to the southern end of the Big Horn mountains. The beds increase in thickness towards the east and the lithological character becomes different, changing from a soft fine shale in the west to a hard sandy rock in the Big Horn region. The Hailey shales lie just above and comformable on the Mowry beds, which Darton (*3*) describes as follows:

"The stratigraphic succession of the formation [Colorado] is uniform throughout. The lowest beds are several hundred feet of dark-colored shale, usually containing toward the base a deposit of sandstone from 2 to 20 feet thick. This is capped by the Mowry beds, consisting of from 100 to 150 feet of hard shales and thin-bedded, fine-grained sandstone of a dark gray color, which on exposure weathers to a characteristic light gray. These rocks are especially characterized by large numbers of fish scales in nearly every bed. They are often so

abundant as to number from five to ten on a surface of six inches square. Owing to their hardness the beds give rise to round-topped ridges of considerable prominence."

FIG. 1. A typical exposure of the Hailey shales on Connant creek, Wyoming. The Mowry beds may be seen on the left in the background.

In those parts of Wyoming where I worked, the Mowry beds stand out as prominent ridges of hard whitish shales which can be readily recognized from a long distance, and on that account serve as excellent landmarks for the identification of a region where the Hailey shales may occur. In thickness the Hailey shales vary from a few feet north of Lander, Wyo., to something over 200 feet in the Big Horn region. "Near Soap Creek the dark shales overlying the Mowry beds are about 200 feet thick," etc. (*6*). In most of their extent the Hailey beds have numerous brown sandy clay concretions which very often contain vertebrate remains. These concretions vary in size from a few inches to many feet in diameter. In the Big Horn region the concretions are stratified into distinct layers, but such is not the case in other places where the horizon was examined.

So far as is at present known the Hailey shales outcrop along the eastern flank of the Wind River mountains, in the Shoshone anticline; in the anticline along Beaver creek near Hailey, Wyo., the type locality; in an anticline north and west of the

Granite mountains, on Connant creek; in a small anticline west of the Rattlesnake mountains; along the northern and eastern flanks of the Rattlesnake mountains. There are extensive exposures on the eastern slope of the Big Horns, and I do not doubt that they occur also to the west of these mountains. In text-figure 1 is given a view of a typical exposure of the Hailey shales, on Connant creek, north of the Granite mountains, Wyoming. On the left of the photograph the Mowry beds stand out in the characteristic ridge.

The vertebrate fauna of the Hailey shales still remains to be accurately determined, but so far as known it is represented by large and small fishes, amphicœlian crocodiles with hollow limb bones, turtles with completely ossified carapaces and plastra like *Toxochelys* and plesiosaurs of two types. The remains of plesiosaurs are in places exceedingly abundant, evidences of no less than fifty-five individuals having been discovered during one summer. Occurring in these deposits, also, have been discovered the remains of three dinosaurs. The remains described below represent one of these animals. The other two are known in one case from a single worn dorsal vertebra found in one of the massive shell-concretions consisting of myriads of gastropod and lamellibranch shells together with plesiosaur teeth and vertebræ, about ten miles north of where the *Stegopelta* remains were exhumed; and in the other case from three caudal vertebræ discovered in the same beds nearly a hundred miles to the east, near the western base of the Rattlesnake mountains.

The *Stegopelta* remains herein described were once encased in one of the brown sandy clay concretions so abundant in this formation, but many years ago it was exposed and by the weathering processes of a long space of time had become reduced to hundreds of fragments. These fragments had washed and rolled down the slope and had been trodden in the mud by cattle so that when first discovered it was discarded as a worthless plesiosaur specimen. When Doctor Williston, however, in cleaning up some of the fragments came across some typical stegosaurian dinosaur teeth, the whole aspect of the matter was changed and every fragment was carefully collected. As boxed the specimen weighed only 450 pounds, of which about two-thirds was bone. It has been a long and tedious task to fit together the scattered and disassociated fragments, but through the combined efforts of Doctor Willis-

ton and myself a number of elements of the skeleton have been reconstructed.

The specimen as it now stands consists of the following parts: Fragments of the upper and lower jaws with a dozen or more teeth, most of which are fragmentary; seven fragmentary dorsal vertebræ; portions of the sacrum; two caudal vertebræ; many fragments of the ribs; a complete ulna belonging to the left side; portions of the right ulna; portions of the radii; the left ilium nearly entire; a part of the right ilium, showing the acetabulum; the right pubis nearly entire; a portion of the left pubis; the lower portion of the right tibia; the upper and lower ends of the right fibula; many large fragments of the metatarsals; nearly a hundred small bony scutes; several large bony plates, girdles and bony spines representing various portions of the dermal armor; together with a great quantity of waterworn fragments which it is impossible to determine.

The remains described as *Stegopelta landerensis* indicate a stegosaurian dinosaur about two-thirds the size of *Stegosaurus ungulatus* Marsh. The head was small, as is indicated by the size of the teeth. The fore limbs were not relatively so large as in *Stegosaurus*. The entire pelvic region was covered with a dorsal shield of rather thick, scrobiculate plates with elevated centers which are asuturally united over the pelvis. On each plate there is found, either on one side or in the central eminence, a pit, which possibly supported a more or less elongate horny spine. Anterior to the pelvic shield there were many dermal plates and scutes of various sizes scattered over the dorsal region of the body. The anterior portion of the animal appears not to have been armed. Back of the pelvis there were massive dermal plates, huge bony spines and a bony girdle probably encircling the tail in some such manner as in the glyptodonts. The neural spines of the caudal vertebræ were probably each surmounted by an elongate bony plate which quite possibly bore a horny excrescence of some kind. While closely similar in many respects to *Polacanthus*, *Stegopelta* shows wide structural differences from that form, although it must have had much the same appearance as Nopsca (5) has figured in *Polacanthus*. The present dinosaur, in life, may have stood nearly seven feet high at the hips and attained a length of sixteen to eighteen feet. Armed as it was with horns,

spines and excrescences it must have been a bizarre creature, even in those Cretaceous days.

The teeth (plate LVI, figs. 4 and 5) of *Stegopelta* are typically stegosaurian. There are a dozen of them in more or less perfect state of preservation. They are all of practically the same size and character, showing but little variation among themselves. The crowns of the teeth, which measure 7 mm. in breadth, are subcompressed and narrowly palmate with eight radiating costæ, all of which end at the tip in sharp points. The roots of the teeth measure 15 mm. from the base of the crown to the tip of the fang. In point of size and number of costæ the present teeth are so closely similar to those described by Leidy (*5*) as a supposed lacertilian form, *Paleoscincus*, that had the teeth only been found they would undoubtedly have been referred to that genus. It is possible that *Stegopelta* may eventually prove to be a *Paleoscincus* form. This, however, is hardly probable, on account of the great interval of time separating the strata which have yielded the two specimens, *Paleoscincus* occurring as it does near the top of the Fort Pierre Cretaceous and *Stegopelta* near the top of the Fort Benton. Were the form one of a stable group this might not be sound reasoning, but in a group of animals which evolved so rapidly as did the dinosaurs one would hardly expect a genus to continue for so long a time. At all events, the name *Stegopelta* may be retained until more evidence is forthcoming concerning *Paleoscincus*. If, as Hatcher believed (*23*), Lambe's *Stereocephalus* is a *Paleoscincus* form, then *Stegopelta* is a good genus, since it shows wide structural differences from the form which Lambe has described. The tooth which Lambe (*7*) has figured on page 57 certainly resembles those of *Paleoscincus*, and if the tooth really is to be associated with the remains described as *Stereocephalus* a question might arise as to whether these remains were not in reality portions of the skeleton of *Paleoscincus* as Hatcher intimated. Lambe (*8*) says the tooth provisionally associated with the *Stereocephalus* remains "differs from those of the Red Deer river district, referred to the two species of *Paleoscincus*, and is about twice as large as those of *P. costatus*." Just how it differs he does not say, and one is at a loss in attempting to separate the forms from his figures. Size alone is usually no safe criterion for the separation of animal forms, and more particularly genera. I

can but agree with Hatcher that the tooth figured as *Stereocephalus* resembles the teeth of *Paleoscincus*.

The *vertebral column* is represented by posterior dorsal vertebræ, portions of the sacrum and two caudal vertebræ. The remains are more or less fragmentary, but enough is preserved to give a fairly accurate idea of this portion of the animal's anatomy, although it is impossible to determine the vertebral formula.

The *dorsal vertebræ* (plate LVIII, figs. 5 and 6) obtained are twelve in number, for the most part imperfectly preserved. They are cylindroid in form, very slightly amphicœlous, nearly amphiplatyan, and the arches are elevated as in *Stegosaurus* and *Polacanthus*. The centra are slightly excavated below the base of the neural arch as in *Scelidosaurus*. The neural canal is small and is wider in the ventral than in the dorsal portion. The centra measure 60 mm. in width by 70 mm. in length.

The *sacrum* (plate LIX, figs. 6 and 7) as preserved consists of two sections. One includes three firmly coössified vertebræ of the posterior end and the other a part of the anterior end representing two vertebræ. The anterior section measures 120 mm. in length by 70 mm. in width at the widest part. The fragment is very smooth and of a dense bony texture. The neural canal is broad posteriorly but narrows somewhat anteriorly. In plate LIX, figure 2, is represented a cross section through this fragment to show the sacral enlargement at the posterior end. The portion representing the posterior end of the sacrum (plate LIX, figure 7) measures 203 mm. in length by 64 mm. in width at the caudal end. The texture of this part is very fine and compact externally, but internally there is a tendency to a cancellated structure. An interesting characteristic of this element of the skeleton is the high degree of coössification of the various elements composing it. There is not the slightest indication of a suture where the different vertebræ have become joined so that the sacral centra are constituted in a solid bony rod tapering somewhat at the anterior end, as do the sacra of *Polacanthus* (*9*) and *Hylæosaurus* (*10*). The attachments for the sacral ribs are large, and are placed about midway dorso-ventrally of the centra of the sacrum. While the sacrum of *Stegopelta* resembles in a great measure that of *Polacanthus*, yet it varies from it in that the elements composing it are more highly coössified. This condi-

tion cannot be entirely attributed to the age of the individual but is expressive rather of the higher specialization of the present form.

Attached to the neural spines of the sacral elements was a long, narrow dermal plate (plate LVI, fig. 3), evidently in firm union with them. This plate occupied the mid-dorsal line of the great pelvic shield and lay between the iliac armor of the two sides. The plate, like all the rest of the dermal skeleton, is scrobiculate and somewhat of the texture of woven cloth, as Marsh has described in *Nodosaurus textilis* (*11*). It becomes slightly expanded posteriorly, where it measures 30 mm. in width.

The *caudal vertebræ* (plate LIX, fig. 1, and plate LVIII, fig. 3) vary to a remarkable degree from those of the dorsal series. They are greatly compressed dorso-ventrally; are very short, with the sides much rounded and the centra plano-convex. The vertebræ have strong transverse processes. In neither specimen is the neural spine preserved, so it is impossible to say as to its extent. This, however, may be inferred to have been low and stout, if one may judge from its broken bases. The neural canal is not large, measuring only 14 mm. in diameter. The centra measure 82 mm. in width by 38 mm. in length by 41 mm. in height. It is thus seen that the caudal vertebræ are more than twice as wide as long. This condition is not a unique one, since Hulke (*12*) has described the same condition in *Polacanthus*.

The *ribs* are all so fragmentary that no discussion of them can be given. Many of the fragments are triangular in cross section, agreeing in this respect with other armored dinosaurs. Attached to some of the rib fragments are found small bony scutes. The fact is of service in determining the position of these dermal scutes on the body of the animal.

The *ulna* (plate LIX, figs. 8 and 9) of the left side is preserved complete. It shows considerable variation from anything hitherto described for any other armored dinosaur. The shaft of the bone is flattened from side to side and is twisted from right to left. It ends in a rather pronounced expansion distally. The coronoid process is quite prominent and is excavated to form a large sigmoid cavity. The olecranon is long, measuring 70 mm. in length from the base of the coronoid process to the proximal end of the bone. It is flattened from

side to side and ends rather broadly, not in a point as does the ulna of *Stegosaurus*. Viewed from in front the ulna curves strongly outward, especially toward the distal end. It is not so straight as in *Stegosaurus*. The articular surface for the humerus is small. The radial articulations are, however, well marked, with the upper one forming a distinct fossa below the coronoid process. The lower articular surface of the ulna is well rounded and is oval in outline. The ulna measures 385 mm. in total length, 106 mm. antero-posteriorly at the widest part, 45 mm. near the middle of the bone and 60 mm. at the proximal end.

The *radius* is represented by fragments only. The head of one of the elements is nearly circular in outline and measures 60 mm. in cross section. The articular surface is so abraded that it is impossible to determine its form.

The *ilia* (plate LV) are both represented in the collection. The left one is preserved nearly entire. Enough is present to determine the total length and breadth of the bone, and the missing parts have been restored, as is evident from the photograph. The portion of the right ilium preserved shows the acetabulum. The description of the ilium will, however, be confined to that of the left side. The bone is elongate and slightly convex upwards; the convexity becoming strongly pronounced on the outer side. It is 50 mm. thick at the acetabulum, but thins to 5 mm. on the inner side and at the anterior end. The thinning is gradual in these two directions. On the outer edge, however, the bone remains thick for over three-fourths of its length, when it gradually thins, but not so much as on the inner edge. The entire dorsal surface of the ilium is covered by a mosaic of thick, bony, scrobiculate plates firmly united to it. These plates are more or less pentagonal in shape and are not all of the same size. On nearly all there occurs, on some in the center, on others near the edge of the plate, a pit, which in life may have supported a more or less elongate horny spine. When the pit is central it is located in the top of the central eminence which occurs on all of the plates. The plates were once, apparently, suturally connected, but there is now no indication of a suture. They form one continuous bony mass over the entire dorsal surface of the ilium. The diameter of the individual plates varies from 56 mm. to 105

mm., and they are all from 5 mm. to 15 mm. in thickness. A single plate is shown natural size in plate LVI, figure 8.

The lower surface of the ilium is nearly smooth. The only irregularities are the acetabulum and small ridges for muscular attachments. It is gently concave, the concavity becoming stronger towards the outer edge. The acetabulum is in the shape of an elongate oval and is defined by a high ridge of bone. The acetabular cavity is rather shallow and is deeper anteriorly than posteriorly. Its length is 190 mm. and the width, as preserved, is 82 mm. It may have had a somewhat greater width, but not to exceed 90 mm. at the most. The entire ilium measures 48½ inches in total length, 10½ inches at the widest part, and 8½ inches near the middle of the bone.

The ilium must have had a horizontal position during life, for the position of the acetabulum is such that the femur could not have articulated in it had the bone been in any other position. This condition is not exceptional among dinosaurs, since the ilia of *Polacanthus* had a similar position and the ilia of *Triceratops* are horizontal to a much less extent. The articular surfaces for the pubes and ischia have been broken away and lost, so it is impossible to determine the relations of these elements. However, they must have had much the same relations as Seeley (*13*), Lydekker (*17*) and Hulke (*14*) have described for *Polacanthus*.

The *pubes* (plate LVIII, figures 1 and 2) are both represented, the right one nearly complete but lacking the entire post-pubic process. This element resembles more nearly that of *Claosaurus* (*15*) than it does that of its nearest allies, *Polacanthus* (*13*) and *Stegosaurus* (*16*). In form the bone is elongate, flattened and spatulate. It curves gently inwards and is only slightly twisted. In thickness the pubis is nearly uniform, becoming thickened proximally to support the pectineal process (ectopubis of Baur). The pubis measures 300 mm. exclusive of the pectineal process, which is 57 mm. in length. In width the bone measures 112 mm. at the widest part and 86 mm. at the distal end. The external surface of the pubis is crossed by a diagonal ridge for muscular attachments. The post-pubis is not represented in the collection save by a fragment which may represent the disal end. The place where the process has been broken from the pubis is large, so the post-pubis may have been of some extent.

The *tibia* (plate LVIII, figure 4) is represented by the lower end of the bone belonging to the right side. Firmly coössified with it is the astragalus, which rises into a rather prominent ascending process on the anterior surface. The union of the astragalus with the tibia is so complete that were one to view the specimen from the posterior side its presence would never be suspected. On turning the bone over, however, the astragalus is distinctly seen, as is shown in the figure. The spine of the astragalus is broken off, but judging from the groove for its reception it must have been nearly 80 mm. in length. It measures 50 mm. in width at the base. The tibia measures 145 mm. in width distally. The articular surface is broad and pulley-shaped. There is a broad, shallow, trochlear groove which is bounded by two rounded projections. The groove runs up prominently on the posterior surface of the bone but is not so prominent on the anterior surface. From the narrowness of the broken surface of the bone, only 50 mm. in diameter, one would judge that the shaft of the tibia was very slender as described by Hulke (*18*) in *Hylæosaurus* and in *Polacanthus* (*19*). It resembles these forms also in that the shaft of the tibia is triangular in cross section, forming in this case a nearly isosceles triangle. The section shows a marked difference between the exterior of the bone, which is smooth and compact, and the interior, which is coarsely cancellated.

The *fibula* (plate LIX, figures 4 and 5) is represented by the proximal and distal portions of the bone belonging to the right side. The proximal end, which is subtriangular in cross section, measures 85 mm. in width and is considerably expanded as compared to the shaft. The upper end is so weathered that no traces of the rugose surface for the attachment to the tibia are left. However, one side is flattened as if for such a union. The external side of the head is marked by a rather prominent condyle, which projects some 5 mm. from the surface. The shaft of the bone is very slender. At a distance of five inches from its upper end the fibula measures 20 mm. by 30 mm. in diameter being thicker antero-posteriorly than from side to side. In structure the fibula is much like that of the tibia, already described. The distal end, also, triangular in cross section, is of the same proportions as the proximal end.

The *metatarsals* (plate LVIII, figure 7) are represented by

several fragments. The proximal and distal ends of one of them are preserved so that a reconstruction is possible. These fragments represent a rather elongate, slender element with the upper surface rounded and the lower surface somewhat flattened. The proximal articular surface is widely concave and the distal end is pulley-shaped. It is thus evident that the metatarsal is not different from that of other herbivorous dinosaurs. The length of the bone as restored is 150 mm., the breadth of the proximal end is 80 mm., and the height 60 mm.

The *dermal armor* consists of small bony scutes, large dermal spines and heavy plates, all of various shapes and sizes. Mingled in with the other bones of the skeleton were more than four score small bony scutes (plate LVII), varying in diameter from 15 to 75 mm. and of various thicknesses from 4 to 20 mm. The scutes are all scrobiculate and are for the most part rounded, though some are elongated, one scute before me measuring 60 mm. in length by 30 mm. in breadth. The majority of them possess a ridge asymmetrically placed, which runs nearly the entire length of the scute. Others run up to a point in the center; others are flat.

In structure all of the scutes are of a coarsely cancellated character, such as Hulke has described for the scutes occurring in *Polacanthus*. Associated with them were many fragments of heavy triangular ribs with which some of the scutes were firmly united. From this fact it would appear probable that the scutes were scattered along the back of the animal anterior to the great pelvic shield. The elongated scutes referred to above may possibly have been situated on the neural spines of the vertebræ, as in *Scelidosaurus* (*20*). The larger scutes, some of which are as large as the palm of one's hand, were very probably located near and anterior to the great pelvic shield.

Scutes very similar to these described for *Stegopelta* are found in a number of different armored dinosaurs as well as among the crocodiles. There are really no structural differences between the scutes of *Stegopelta* herein described and those found in the common Mississippi alligators. The pittings on the *Stegopelta* scutes are, however, smaller than in the latter. Hulke (*21*) has described a few scutes belonging to *Polacanthus* which resemble the present specimens very much. Lambe (*22*) has figured three scutes associated with the form *Stereo-*

cephalus which are almost identical with the scutes of *Stegopelta*. Hatcher (*23*) was certainly in error in criticizing Lambe's association of these scutes with dinosaurian remains and in claiming that they were of a crocodilian nature, since in the present specimen there can be no doubt as to their dinosaurian character. Nopsca (*24*) has also fallen into the same error as did Hatcher when he says that crocodilian remains were associated with the *Polacanthus* specimen. Seeley (*25*) has described and figured scutes similar to the above in *Crateomus*. Huxley (*26*) has described and figured identical scutes in *Acanthopholis*. Marsh (*27*) has figured some small bony scutes in *Triceratops*. Owen has figured scutes of a like nature in *Scelidosaurus* (*20*). Possibly other armored dinosaurs possessed such scutes.

The question of the morphological value of these scutes is an interesting one. Judging from the scutes in *Stegopelta,* one would incline to the opinion that they represent the rudiments of a complete bony armor which in time, had the dinosaurs survived, might have covered the whole dorsum of *Stegopelta's* descendants. Such a suggestion might apply equally well to our modern crocodiles. It is pretty certain that the scutes in the crocodiles are not vestigial, since it is not now conceded that the modern Crocodilia are descended from the ancient armored teleosaurs (*28*).

The *dermal spines* (plate LVI, fig. 1, plate LIX, fig. 3) are all of a dense bony texture with the external surface pitted. A portion of a small dermal spine is represented, natural size, in plate LIX, fig. 3. Its base is broken away so it is impossible to determine its extent, but this was, in all probability, not considerable. One of the most peculiar portions of the dermal armor is that represented in plate LVI, fig. 1, which is called a large dermal spine, and which I have provisionally located near the base of the tail. The spine is asymmetrical and is lateral in position, having had a mate on the opposite side of which nothing remains.

The spine preserved is much broken and the distal tip is lost. As reconstructed it is of massive proportions in comparison to the rest of the exoskeleton. In cross section it is for the most part triangular, with two sides of the triangle concave and one convex. It is rounded near the distal end. The spine, unlike most elements of a similar nature, is bifid, as is represented in the figure (plate LVI, fig. 1). The short

spine measures 80 mm. from the point of its inception to the tip, and the main spine measures 16 inches from tip to tip. At its widest part it is 100 mm. in breadth. The surface of the bone is pitted with irregularly placed cavities as though it were encased with horny substance.

The exact position of this large spine on the body of the animal is, of course, largely a matter of conjecture, since it was found broken and disassociated and mingled with various other parts of the skeleton, but it seems best to locate it back of the pelvic shield, since the caudal vertebræ are much stouter than the dorsal ones and since there is no evidence of any armor excepting the small bony scutes anterior to the pelvis. The spine is totally unlike anything described for any other stegosaurian dinosaur.

The *dermal plates,* represented in plate LVI, figs. 2 and 9, are massive and of a compact texture. Their position on the skeleton is a puzzle. The plate represented in plate LVI, fig. 9, is not entire. It is asymmetrical, one side being crossed by a rather high ridge. Its upper surface has pittings and grooves. The under surface is smooth and rounded. It is possible that this is a portion of another girdle similar to the one described below. That it is not a part of that girdle is evident from its proportions. The plate measures 105 mm. in diameter. The other dermal plate (plate LVI, fig. 2) is apparently complete, with a broad surface for articulation with some element which is now lost. This plate is concavo-convex. It measures 140 mm. across in the longest diameter. It is without vascular markings of any kind, but is smooth as though it were entirely embedded in the flesh of the animal.

The part of the *girdle* represented in plate LVI, figs. 6 and 7, is like the last described plate in that it is of a compact texture. In the girdle the upper surface is pitted, and crossed at regular intervals by rather high ridges the sides of which are slightly concave. This bone at once reminds one of the similar element figured and described by Lambe (*29*) as occurring in the *Stereocephalus* form. Lambe (*29*) however, located the girdle back of the head, and if his interpretation of the large fragment which he calls the skull is correct such a location would be quite plausible. The present girdle differs in a great degree from that described by Lambe, since it is asymmetrical and had a mate on the opposite side, of which there are fragments in the collection. It differs further in being a solid mass

of bone instead of a bony ring to which the scutes are united. The girdle as preserved is in the form of an arch and is composed of three plates, only two of which are ridged. The under surface is smooth and longitudinally convex. The part of the girdle preserved measures 320 mm. in length and 110 mm. in width.

Stegopelta finds its nearest allies in *Polacanthus,* from the Wealden of the Isle of Wight; in *Paleoscincus,* which must, I think, include the *Stereocephalus* of Lambe, from the Belly river deposits; and *Stegosaurus,* from the Lower Cretaceous of Wyoming and Colorado. The characters which separate *Stegopelta* from *Stegosaurus* and *Paleoscincus* have already been considered. From *Polacanthus* the present form differs in the whole surface of the ilium being covered in the former animal with a firm mosaic of very small, somewhat rounded, plates, which are scarcely at all sculptured, as I learn from Doctor Williston, who has examined the type specimen. These plates in *Stegopelta* are relatively quite large and strongly sculptured. The present form differs from *Polacanthus* also in the divergence of the points of the ilium anteriorly. In *Polacanthus* the iliac region was entirely covered by a bony shield, but in *Stegopelta* this shield was not continuous, but there was a space between the anterior ends of the ilia which was filled, probably, with small bony scutes. There have been many stegosaurian dinosaurs described from various parts of the world, notably North America and Europe. The group seems to have had a very wide distribution geographically.

In conclusion, I wish to express my gratitude to Dr. S. W. Williston, not only for his kindness in turning over the material to me for description but for his kindly interest and help during the entire investigation.

The specimen is in the Walker Museum, University of Chicago.

Since the above was written there have appeared two papers describing two new types of dinosaurian reptiles closely allied to the above-described form. One of these papers,* from the American Museum of Natural History, is of especial interest, since the material supplements in an excellent way that which has just been described. Mr. Brown's restoration of the *Ankylosaurus magniventris,* while based in large part on Marsh's

* Brown, Barnum, 1908. Bulletin Amer. Mus. of Nat. Hist., vol. XXIV, p. 187.

drawing of *Stegosaurus ungulatus,* is not accurate as to the form of the animal. The pelvic region was undoubtedly covered over with a heavy shield as in *Stegopelta.* Indeed, Doctor Williston† says, "*Ankylosaurus* is either very closely allied to or identical with *Stegopelta* Williston, a genus overlooked by Mr. Brown."

The remains described by Mr. Brown consisted of a skull, some small dermal scutes, a few vertebræ, a scapula, a few ribs and other parts, most of which were lacking in the above-described animal.

Dr. O. Abel has given (Verhandl. d. k. k. Zoöl.-bot. Gesell. in Wien, Bd. LVIII, p. 215, fig. 3) a restoration of *Ankylosaurus magniventris* Brown. It is to be doubted if he has added to our knowledge of dinosaurian attitudes, since the reader is at once struck with the grotesque and impossible attitude which he has caused the animal to assume. It is unfortunate that Brown's ideas of the arrangement of the scutes on the back should have been given by Doctor Abel, since there is not the slightest evidence that they assumed anything like the arrangement he has represented.

The other dinosaur is from the Niobrara Cretaceous of Kansas and was collected by Mr. Charles Sternberg in the Hackberry creek region.

Doctor Wieland‡ describes these remains as *Hierosaurus sternbergii,* new genus and species. This form is also doubtfully distinct from *Stegopelta,* unless it be that the skeletal characters were widely at variance to the characters of the dermal plates. A comparison of figure 9, plate LVI, of the present essay, with Doctor Wieland's figure 6, will show how very closely the dermal elements of the animals resemble each other. Comparisons also of the figures on plate LVII of the present paper with Doctor Wieland's figures 2, 4 and 5 will reveal the close similarity of the small dermal elements. It would, however, be too previous to say certainly that *Hierosaurus* and *Stegopelta* are identical. The geological horizon of the two specimens is certainly not far apart, or perhaps identical, since the Hailey shales occupy relatively the same position in Wyoming as the Niobrara chalk does in Kansas.

† American Naturalist, vol. XLII, No. 501, p. 629.

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CONTENTS:

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BY ROY L. MOODIE.

(Contribution from the Zoölogical Laboratory, No. 191.)

Plates LX to LXII.

THERE have been, during the past few years, several additions to our knowledge of the soft parts of extinct animals. This knowledge has to do, in large part, with the firmer tissues, such as the cartilaginous portions of the skeleton, the skin, the muscles, but in some cases the kidneys, oviducts, nervous tissues, blood vessels and alimentary canal are clearly preserved. Dean (*1*) has been especially fortunate in the discovery of some of these structures in the sharks of the Cleveland shales of Ohio. He has described very fully the preservation of the kidneys, muscles, skin, the cartilaginous elements of the fins and arches and portions of undigested food. So perfectly are the remains preserved that the tissues, in some cases, admit of histological differentiations into the component elements. Eastman (*2*) has described the preservation of the outline of some acanthodians from Mazon Creek. Woodward (*3*) has contributed to our knowledge of the soft anatomy of fossil fishes in many ways and has added interesting information on the anatomy of the lateral line system of Cretaceous selachians. Jaekel (*4*), Dean (*1*, p. 267) and Gill (*5*) have discussed the anatomy and the significance of Jurassic and Cretaceous chimæroid egg cases. Otto Reis (*6*) has written much on the soft anatomy of various fossil fishes, more

especially the Cœlacanthidæ, in which he has described the form of the muscle fibers, the swim bladder and other structures. Eastman and Parker (*21*) have described the preservation of the brain, the internal ear and arterial vessels in *Rhadinichthys deani* Eastman from the base of the Waverly shales, Kentucky. Dean (*20*) has mentioned the preservation of the lateral line sensory canals of the head, the auditory organ and the rim of the nasal capsule in *Acanthodes bronni* from the Permian of Lebach, preserved in the Berlin Museum. Fritsch (*7*) has described very accurately the outlines of the body and fin membranes of *Pleuracanthus*. Traquair (*8*), Dean (*1*) and Sollas (*9*) have added to our knowledge of the anatomy of *Paleospondylus*. Patten (*10*), Eastman, Traquair and others have written on various structures of the Ostracophores. Other authors have contributed from time to time on the subject, until we have, in some instances, *e. g.*, *Bothriolepis*, *Paleospondylus*, *Cladoselache*, a fairly definite idea as to the outward form and internal structure of the creature. Among higher animals something has been done on the soft anatomy of the extinct Amphibia, Ichthyosauria, and Dinosauria.

It is with some degree of pleasure that the writer is able to add to the knowledge of the soft anatomy of extinct forms by the discussion of the alimentary canal of two Cretaceous fishes. One is a species of *Empo*, probably *E. nepaholica* Cope, from the Niobrara Cretaceous of western Kansas, and the other is a new species of clupeoid fish from the Cretaceous of Texas.

The specimen which probably belongs to *Empo nepaholica* Cope consists of the cast of a large stomach which, in all probability, represents a fish of some ten or twelve feet in length. It is No. 347 of the University of Kansas Paleontological Collection. The remains were discovered in 1897 by Mr. H. T. Martin in the Niobrara chalk four miles northwest of Elkader, Kan. The specimen has recently been presented to the Museum of the University by Mr. Martin.

The specimen consists of a cast of the larger portion of the alimentary canal of a large species of fish. Attached to the matrix of the cast on one side is the major portion of the right pectoral fin, which is described and figured below. So far as the writer is aware, the present specimen is the most perfect example of the pectoral limb of an *Empo* which has been de-

scribed. Cope (*18a*) figured an incomplete one and Hay mentioned another. Hay (*11*) has figured a portion of the caudal fin of an *Empo* showing the extreme character of segmentation of the rays. The same character is shown in the pectoral fin.

The stomach is rounded, somewhat laterally compressed, and elongate in a slightly U-shaped curve. There are eight muscular constrictions on the ventral surface and four on the dorsal. The constrictions, on the ventral surface, occur in groups. Anteriorly there are two close together. This group is separated by a space of an inch and a quarter from the next group, in which there are three, which occur a little over one-half inch apart. The last group, also of three, is separated from the second group by one inch. The surface of the stomach cast is covered with a dark, apparently carbonaceous, material which may be carbonized muscle, together with a few large scales of the typical *Empo* form. Running the entire length of the specimen are longitudinal ridges and grooves showing the cast of the muscular walls of the stomach.

The interior of the stomach, in cross section, shows no food material, but only chalk. It is possible that the fish, like some of its modern relatives, may have been a bottom feeder and its stomach may have been partly filled with Niobrara mud at the time of its death. There must, however, have been some sediment enter the stomach after death, for the full form of the organ is preserved as though the entire stomach cavity had been packed with mud. Furthermore, the form of the stomach is that of a carnivorous fish, and recalls very strongly the stomach of a mountain trout or of the sunfishes of our inland streams, all carnivorous in habit.

The portion of the alimentary canal preserved is in two lobes. The first lobe is undoubtedly the stomach proper, and the constriction between the lobes is the pyloric region. The other lobe is unlike anything among modern fishes with which I am at present acquainted. It is undoubtedly an enlargement of the intestine and possibly served as a secondary stomach. It lacks the muscular constriction and the longitudinal plicæ. The plicæ are, however, continued well across the pyloric region to the beginning of this second enlargement.

The pectoral fin, as preserved, is well characterized in the photograph (plate LXII, figure 2). It is somewhat turned in-

ward and bent, during interment, back against the stomach. There are eleven rays preserved. The anterior rays are cross segmented with long divisions, which measure 7 mm. in length in the second ray. The square notches mentioned by Hay (*11*, p. 87) as occurring on the specimen of *Empo nepaholica* Cope in the United States National Museum, are entirely lacking from that portion of the anterior ray which is preserved in the present specimen. The teeth on the edge are also absent, nor do I find that they are evident in Cope's figure referred to by Hay. The figure is very indistinct, and if the notches were present they could not, in the nature of the case, be normal, but would represent places where the segments had dropped out. The first ray is not a spine. In other respects the present specimen agrees well with that figured by Cope on plate LII, figure 1 (Cretaceous Vertebrata). The fifth and succeeding rays are segmented like the anterior ones, but the segments are smaller and measure, on the average, only about 2 mm. The seventh ray is especially broad, equaling in its proportions two and one-half of the other rays. All of the rays are split distally. The seventh divides into four secondary rays and the divisions ascend more and more to the base of the fin posteriorly. The fin supports are obscured by scales and matrix so that their nature cannot be determined. On the opposite side of the specimen, below the pectoral fin, there are large scales and fragments of ribs.

The second intestinal enlargement is interesting, entomologically, as showing the borings of some fossorial hymenopteron; possibly some one of the smaller species of the Andrenidæ. There are fragments of pupa cases in the burrows, so there is no doubt as to the recent origin of the holes.

The present specimen is so far the only remains known of the soft anatomy of the Kansas Cretaceous fishes, and, so far as I can learn, the first indication of the alimentary canal of Cretaceous bony fishes of any region. Whether the stomach and intestines in their various forms will ever be of any help in determining the relationship of the various osseous fishes remains to be determined. It is to be feared, however, that the fishes have been so diversified according to food habits that these structures will not be of any great phylogenetic value. The remains are interesting, however, as indicating, in a measure, the habits of life of at least one of the Cretaceous fishes.

Measurements of the specimen of *Empo nepaholica* Cope:

Entire length of the alimentary canal as preserved	53.2	cm.
Greatest diameter at anterior end	10	
Least diameter, across pyloric region	3	
Greatest diameter of posterior enlargement	7.4	
Length of pectoral fin as preserved	9	
Greatest width of fin	3.7	
Length of first ray	8	
Width of first ray	2	mm.
Diameter of large scale	15	

Thrissopater intestinalis new species.

A species of clupeoid fish is represented in the University Museum by the remains here described as a new species. The form is located in *Thrissopater* of Günther, described from the Gault of Folkstone in 1872 (*12*). My thanks are due Dr. A. Smith Woodward for the suggestion of a comparison of the present form with that of *Thrissopater*. It was thought for a time that the present form represented a genus distinct from *Thrissopater*. The distinguishing character was thought to be found in the position of the pelvic fins, which has served as a generic character in other fishes. In *Thrissopater salmoneus* the pelvic fin is opposite the dorsal and in the present form it is distinctly posterior to it. There is, however, a great range of variation in the position of the pelvic fin, especially among the lower osseus fishes. My thanks are due Prof. E. C. Starks for aid in reference to the characters of the modern bony fishes. During the summer of 1909 the writer spent some weeks studying with him the fishes of Puget Sound. He first called the writer's attention to the wide variation of the location of the pelvic fin in the clupeoid fishes. This variation is easily understood when it is remembered that the pelvic fin lies free from any firm attachment and hence its variation in location would not mean as much as though it were attached to the scapular arch. Further aid was rendered the writer in determining the characters of the clupeoid fishes by Dr. W. G. Ridewood, of London. An examination of the essays of this gentleman has been of great service.

The absence of material for direct comparison with the species of *Thrissopater* makes it best to locate the present form temporarily in that genus. The systematic position of *Thrissopater* has been the subject of a wide variance of opinion. Dr. Günther regarded *Thrissopater* as closely allied to the modern Clupeidæ and located it (*13*) in that family, in which he also included such forms as *Spaniodon, Albula, Elops*

and *Engraulis*, all of which have been regarded by different authors as types of distinct families. Boulenger (*14*) regards *Thrissopater* as a member of the subfamily Thrissopatrinæ, which is one of his four subfamilies of the Clupeidæ. Dr. Jordan (*15*) located the form in the family Spaniodontidæ, which is closely related to the Elopidæ, between which and the Clupeidæ Boulenger regards *Thrissopater* as being intermediate (l. c., p. 564). Professor Starks writes me that Doctor Jordan now regards the family Spaniodontidæ as untenable. Dr. A. Smith Woodward (*16*) regards *Thrissopater* as a member of the Elopidæ, which differ from the Clupeidæ in the possession of a single supramaxillary, the degree of union of the parietals and the gape of the mouth and the presence of a gular plate. The present form presents the characters of the Elopidæ in so far as they are preserved. In recent forms, the presence of a gular plate in the Elopidæ serves as a convenient landmark for the distinction of the families of the Elopidæ and Clupeidæ. As a matter of fact, the families are so closely allied that the characters used for their separation must in time be broken down by the discovery of new material.

Herrings and herring-like fishes are not at all rare in the Cretaceous deposits of the world. Davis (*17*) has described many forms of clupeoid fishes from Mount Lebanon. Before him Agassiz advanced the knowledge of these forms, and latterly Woodward has described several interesting clupeoids. Cope described several clupeoids from the Eocene of Green River, Wyoming (*18*), and Jordan has cited the interesting relations of these forms to forms now living in the rivers of Australia and Chili. At the present time herrings form an important item in the economic history of the world. Huxley has dwelt (*19*) especially on the anatomy and relations of the herring in this connection. The present form adds yet another mite to our knowledge of these interesting fishes. It is believed to be as early as or perhaps somewhat older than many of the described clupeoids. The specimen comes from the Austin shales or limestone, which is a probable equivalent of the Niobrara Cretaceous. It is from near Baylor, Tex., and is No. 300 of the University of Kansas Museum.

The remains preserved consist of the nearly complete fish, as may be determined from an examination of the plate. The caudal portion is, unfortunately, lacking. The outer surface of the skull was badly broken and Mr. Martin very kindly ex-

tricated the skull for me from the matrix. It was a difficult task and the results were hardly worth the efforts, for the embedded portion was but little better preserved than the outer. Enough of the skull is preserved, however, to show many of the important characters. The head is naked; the body compressed, but whether the ventral edge was drawn out into a keel or not cannot be determined from the specimen. The mandible is fully as long as the skull. The relations of the articulation to the orbit cannot be determined, nor can the position of these openings be definitely located. The parietal bones are, apparently, small. Certainly the supraoccipital projects forward as in *Thrissopater magnus*. Maxilla is slender, with a single supramaxillary. The margin of the jaws is provided with a single row of small, recurved, sharply pointed teeth of uniform size throughout the length of the entire mandible and maxilla. The quadrate is broadly V-shaped, with a prominent articular surface. Nasal, ethmoid and premaxillary bones ornamented with numerous small pits. The same character occurs on the anterior end of the maxilla of the right side. A single, squarish, punctate, thick, pharyngeal bone is present. A very few branchiostegal rays are preserved; not over ten. From the relationships of the form we would judge there were many in the complete fish. The opercular apparatus is smooth. Posterior suborbital plate radiately furrowed; its extent exceeding one-third of the length of the skull; remaining elements indistinct. Greatest depth of the body is slightly greater than the length of the skull from premaxilla to supraoccipital. The length of the body is possibly equal to four times the length of the skull. The fins are relatively small. Dorsal fin median in position. The pectoral fin has sixteen rays, which are cross-segmented but are not divided longitudinally. The rays are supported by five baseosts. The distance between the origins of the pectoral and pelvic fins is equal to nearly four times the length of the pectoral fin. The pelvic fins have nine rays, none of which are cross-segmented. The pelvic bone is large and spatulate.

The body scales are small, cycloid, deeply imbricated and marked with fine concentric lines. There is a large, elongated and elegantly sculptured scale at the base of the pectoral fin, as in *Thrissopater salmoneus;* though in the present instance the scale is less than one-half the length of the pectoral fin rays. The vertebræ are preserved to the number of thirty-

four. There may have been as many as forty-five or fifty in the complete fish. They are fully ossified, slightly constricted and marked with small longitudinal ridges. The length is slightly greater than the depth. The neural spines are long and interlock with the interneurals. Supernumerary ribs present. Six of them occupy the space of a single vertebral centrum.

The specimen as preserved is well characterized by the figures. The fish lacks the posterior end of the body back of the anus. It is chiefly remarkable on account of the extraordinary preservation of the casts of the rectum and intestine, of which there are six coils or loops preserved. The remains are embedded on the right side in a calcareous, arenaceous, shaley limestone, which also contains remains of some species of *Inoceramus,* small fish teeth and the base of a moderately large shark's tooth.

Perhaps the most interesting portion of the entire specimen is the intestinal canal, from the presence of which is derived the specific name. In general features the alimentary canal as preserved recalls that of the common fresh-water buffalo fish, *Ictiobus bubalus* Raf (plate LXII, figure 1). The similarity in form is undoubtedly indicative of similarity of habit, and since we know that the buffalo fishes are bottom feeders we can easily predicate that our ancient Cretaceous fish had similar habits and at the time of its death the alimentary canal was filled with mud mixed with some organic substances; for the fossil shows a different texture for the cast of the alimentary canal from the matrix, indicating different materials. The intestine as preserved consists of six coils or loops of the very small intestine which immediately precedes the rectum, which is likewise preserved. The rectum is elongate but no more so than is the same structure in the buffalo fish. The essential characters are shown in the illustrations.

The distinction of this species from the other three which have been assigned to *Thrissopater* is to be found, first of all, in the posterior location of the pelvic fin. Its base lies at a distance posterior to the back edge of the dorsal fin, which is equal to its own length. So far as I am aware the large axillary scale in other species of *Thrissopater* is larger and unornamented. From *T. salmoneus* Günther the present form is to be distinguished by the relative proportions of the head and

body. The head and opercular apparatus is contained only about twice or at most two and one-half times in the body. From *T. magnus* it is to be differentiated by the relative proportions of the opercular and the skull. The former is contained twice in the latter in the present form. In *T. magnus* it is contained three times. The present species is indeed very closely allied to *Thrissopater magnus* Woodward from the Lower Chalk of Hollingbourn, Kent. It is to be distinguished by the relative dimensions of the vertebræ as well as by the proportions existing between skull and opercular. The vertebræ in *T. magnus* are higher than long while in *T. intestinalis* they are slightly longer than high, and the ends are occupied by distinct rims, such as do not occur, apparently, in the English form. The characters which the two species have in common are striking. They both have the same notch in the anterior end of the mandible; the same finely punctate ethmoid and nasals; the same form and dimensions of mandible and maxilla; the same divided posterior suborbital; and the same relative shape of skull. Many of these are generic characters.

The present species can be distinguished from *Thrissopater* (?) *megalops* Woodward by the proportions of the head. In *T.* (?) *megalops* the height of skull from cotylus to supraoccipital is equal to the length of the mandible, while in *T. istestinalis* the mandible exceeds the height of the skull from cotylus to supraoccipital by 15 millimeters. It may be further distinguished by the relative proportions of the pectoral arch and skull as well as by the absence of the radiately furrowed suborbital and the notch in the anterior end of the mandible in *T.* (?) *megalops.*

Measurements of *Thrissopater intestinalis* Moodie:

Length of specimen	29	cm.
Greatest depth	9	
Length of skull (with opercular apparatus)	9.7	
Depth of skull at quadrate	4.8	
Length of mandible	6	
Depth of mandible at cotylus	1	
Diameter of pharyngeal plate	9	mm.
Length of tooth	2.5	
Width of opercular apparatus	3	cm.
Length of clavicle	2.5	
Length of pectoral fin	2.5	
Width of pecoral fin	1.2	
Length of pelvic fin	2.4	
Width of pelvic fin	1.2	
Length of actinost	3	mm.
Length of dorsal fin as preserved	2.1	cm.

Width of dorsal fin as preserved	1.8	
Length of caudal hæmapophyses	9	mm.
Length of vertebræ	6	
Depth of vertebræ	5	
Width of small intestine	3	
Length of rectum	12	cm.
Width of rectum	1.3	
Length of interneural	1	

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CONTENTS:

A New Species of Holotrich, ... *By Nadine Nowlin.*

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A NEW SPECIES OF HOLOTRICH.

BY NADINE NOWLIN.

(Contribution from the Zoölogical Laboratory, No. 193.)

Two text figures.

IN April of 1909 there was brought to my room at the Naples Station a jar of the small barnacle *Lepas pectinata,* and in examining microscopically one of the appendages I observed a minute rotifer-like animal creeping along its edge. This animal, after being studied for some time, was found to be an infusorian—a Holotrich, resembling in a general way Huxley's *Dysteria armata.* Upon careful study, however, it differed in so many ways that I concluded it to be a distinct form.

Symbiosis is such an old and well known condition in the organic world that any discussion of it for its own sake is unnecessary here. As in other cases, these two animals live together, deriving mutual benefit from the combination; the ciliate finding a shelter in the appendages and the barnacle, no doubt, getting a tasty morsel when it succeeds in dislodging the little animal long enough to sweep it into the gullet. It is a question how the protozoön manages to thrive under these conditions. We know that the water currents set up by the host are swift and frequent, and life under such tempestuous conditions would seem worse even than the chances in the open sea. The structure of the smaller organism partially explains this. It has first of all an armature, a tough siliceous skeleton, covering the body, except a narrow strip on the ventral side. With this protection it is not easily crushed. Then caudally there protrudes a hook-like tail, which not only helps the animal in

creeping over the rough surface of the appendage, but also serves as an efficient means of attachment. Near the oral opening protrudes a long flagellum which lashes rapidly to and fro and secures food for the animal.

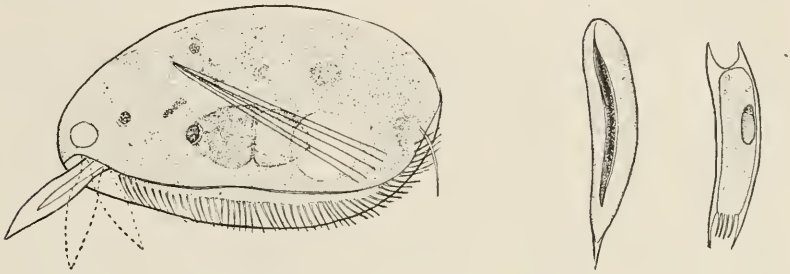
The small visitor thus established on the appendage of a barnacle obtains its food from the currents of water which are constantly coming in to the host. When the dangers come and the appendages are enclosed by the calcareous plates of the barnacle, the ciliate still has moisture and some food. One might think that in casting its lot with a sedentary animal the free-swimming protozoön had limited its opportunities. This is not wholly true. *Lepas pectinata* grows on masses of lava, and during storm these masses become broken and widely scattered. It is only occasionally that the Naples collectors are able to find this barnacle—its appearance in the bay depending upon, first, a storm at sea, and then a strong south wind to sweep it in. During April and part of May I was able to obtain this material but twice. This was unfortunate as the nucleus is an interesting one, and promises well for cytological work. The barnacles live less than a week indoors and the ciliates perish with them. Moreover, the ciliates are not numerous. As a last resort for material, I took barnacles from the storeroom, preserved in formalin, and succeeded in finding the specimens, but they did not prove satisfactory for nuclear study.

DESCRIPTION OF SPECIMEN.

The animal is oval in form, being slightly wider cephalically. It is covered with siliceous skeleton, giving the appearance of a bivalve shell, and possesses a caudal appendage. So different is it from the usual infusor that it is little wonder most zoölogists at first glance pronounce it a rotifer, or a mollusk, or a low crustacean. The animal is flattened dorso-ventrally, the dorsal shell being more extensive and bending over the right side. The dorsal is slightly convex; the ventral is concave and attaches to the dorsal by a deep groove on the left. The right edge of the dorsal shell and the left edge of the ventral do not meet, thus leaving exposed a very narrow strip of protoplasm. This uncovered protoplasm is ciliated and it is by means of these cilia that the animal swims. The surface of both shells is smooth.

The crevice between the ventral and dorsal plate lies then

on the right ventral area of the animal, and because the animal moves often on the edge we are apt to think of this ciliated region as purely ventral. Lankeste in describing the family Dysterina, to which I believe this specimen belongs, calls this the ventral side. The right ventral groove then extends from the posterior end of the animal completely along the side and rounds across the cephalic end. At its caudal extremity is an appendage, and at the cephalic, a long flagellum.



EXPLANATION OF TEXT FIGURES.

The figure to the left is a view of the right dorsal side of the animal, showing the flagellum anteriorly and the ventral cilia; the calcareous supporting rods of the mouth, the two contractile vacuoles and the nucleus. The caudal appendage is shown by a continuous line and its range of motion by dotted lines.

The middle figure is a view of the animal on edge, showing a convex dorsal side, concave ventral, left dorsal groove and caudal appendage.

The right figure is an imaginary cross-section through the nucleus.

The tail, like the body, is covered by the silicious skeleton and appears hollow, at least part of the way. Whether the anus lies at its distal end, as is claimed for *Onychodactylus*, I am unable to say. Its range of movement is nearly 180 degrees in the plane of the right ventral groove. In movement the animal may use this organ as a propeller, shoving itself forward with long strides by placing the end against a solid structure. It is this motion which resembles strongly that of a rotifer. In swimming the tail is usually folded into the groove like a knife-blade closed in its handle, and the animal is carried forward by the vibration of its cilia. The animal when creeping over a solid surface stands on the ciliated edge, much as a mussel when moving through the sand. In swimming it lies slightly on its ventral side and has a swinging motion through the water.

The flagellum is located in a deep depression of the cephalic protoplasm. On superficial examination this depression might

be mistaken for the mouth, but the mouth is just ventral to it and convenient to the currents set up by the flagellum.

The gullet is a long, narrow funnel running obliquely upwards and backwards until it nearly reaches the opposite side of the body. Like other protozoa of this group, it is supported by calcareous rods. These are plainly visible when picro-sulphuric acid is first placed on the specimen, but very soon the acid destroys them and the gullet shows only as a clear place in the protoplasm.

Two contractile vacuoles are present, and a very large nucleus. The nucleus is especially interesting in these forms because the meganucleus is heterogeneous, the anterior half remaining almost clear when stained with picro carmine, the posterior half staining densely. The micronucleus may lie quite far to the posterior end of the meganucleus. The fact that the two halves of the nucleus react differently to the same stain suggests a segregation of functions. Since in division the meganucleus breaks transversely, the resulting animals are dimorphic as to meganuclear protoplasm.

CLASSIFICATION.

According to Lankester's classification the specimen described above belongs to the sub-order Gymnostomata, that division of the Holotrichs in which the mouth is closed in the intervals between the acts of ingesting food. It belongs to the family Dysterinæ (Clap. & Lach.), which corresponds to Calkins's sub-family Ervilinæ: Cilia confined to ventral surface or a portion of it; caudal end invariably possesses a movable style arising from caudo-ventral surface.

Of the various genera grouped under this family, or sub-family, our specimen corresponds most closely to the last of the following list:

Ægyria (Clap. & Lach.), 1858.
Onychodactylus, Entz, 1884.
Trochilia, Duj., 1841.
Dysteria, Huxley, 1857.
Dysteropsis, Roux, 1902.

The only species of this genus, so far as I can learn, is the small one found in the lakes of Geneva and called minuta by Roux, because it measures only 28 micra long and 16 micra wide. The animal described in this paper is marine; the av-

erage specimen is 83 micra long and 50 wide. Its habitat in the tentacles of *Lepas pectinata* suggests the name of *Dysteropsis pectinata* for the new specimen.

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CONTENTS:

ORTHOPTERA FROM THE SANTA RITA MOUNTAINS, ARIZONA, COLLECTED BY THE UNIVERSITY OF KANSAS EXPEDITION, *James A. G. Rehn.*

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ORTHOPTERA FROM THE SANTA RITA MOUNTAINS, ARIZONA, COLLECTED BY THE UNIVERSITY OF KANSAS EXPEDITION.

BY JAMES A. G. REHN.
Academy of Natural Sciences of Philadelphia.

Plate LXIII.

THE collection forming the basis of this paper was made in the Santa Rita range during the summer of 1907 by the University Museum expedition under the late Prof. F. H. Snow.

FORFICULIDÆ.

Spongophora apicidentata Caudell.

Santa Rita mountains, 5000 to 8000 feet, July. F. H. Snow. One female.

This species has previously been recorded from localities in Arizona ranging from near a hundred feet to about five thousand feet above sea level.

BLATTIDÆ.

Ischnoptera notha Rehn and Hebard.

Santa Rita mountains, 5000 to 8000 feet, July. F. H. Snow. One female.

This specimen agrees with an individual of the same sex from the Huachuca mountains previously examined by the author.*

The measurements of the Santa Rita specimen are as follows:

Length of body	14.0 mm.
Length of pronotum	4.5
Greatest width of pronotum	5.9
Greatest width of tegmen	4.5
Length of tegmen	10.0

* Proc. Acad. Nat. Sci. Phila., 1907, p. 25 (*Uhleriana*); Rehn and Hebard, Ibid. 1910, p. 443.

In Arizona this species appears to be restricted to certain elevations on mountains of the southern part of the territory, viz., Santa Rita, Huachuca and Patagonia ranges.

Blattella dilatata (Saussure).

Santa Rita mountains, 5000 to 8000 feet, July. F. H. Snow. One female, one male.

These specimens agree with those recorded by the author* from the Huachuca mountains.

MANTIDÆ.

Bactromantis virga Scudder.

Santa Rita mountains, 5000 to 8000 feet, July. F. H. Snow. One female.

This specimen is slightly larger than a Huachuca mountains individual of the same sex.

PHASMIDÆ.

Pseudosermyle truncata Caudell.

Santa Rita mountains, 5000 to 8000 feet, July. F. H. Snow. One female.

Parabacillus coloradus Scudder.

Santa Rita mountains, 5000 to 8000 feet, June. F. H. Snow. Two males, one female.

ACRIDIDÆ.

Telmatettix aztecus Saussure.

Santa Rita mountains, 5000 to 8000 feet, June. F. H. Snow. One male.

Mermiria texana Bruner.

Santa Rita mountains, 5000 to 8000 feet, July. F. H. Snow. One female.

Prorocorypha,[1] n. gen.

Allied to *Paropomala* Scudder, but differing chiefly in the great development of the cephalic portion of the head, the greatly elongate supra-anal plate of both sexes and the sub-genital plate of the male.

Body sub-bacilliform. Head greatly elongate; vertex and pre-ocular region strongly produced into a rostrate process, fastigium lanceolate, tectate, carinate; antennæ, at least of male, somewhat triquetrous, subensiform. Cephalic and median limbs very small. Caudal limbs very slender. Pro-

* Proc. Acad. Nat. Sci. Phila., 1907, p. 26.

[1] $\pi\rho\omega\alpha$, prow; $\kappa o\rho\upsilon\phi\eta$, head.

sternum with a median compressed protuberance; mesosternal lobes contiguous. Supra-anal plate aculeate in both sexes; subgenital plate of male strongly produced, knife-like.

Type: *P. snowi*, n. sp.

Prorocorypha snowi n. sp. (Plate 63.)

Types: ♂ and ♀ (not mature); Santa Rita mountains, Pima and Santa Cruz counties, Arizona, 5000 to 8000 feet, June (♂), July (♀), 1907. F. H. Snow. (University of Kansas.)

Size medium; form very elongate. Head one and one-half times the dorsal length of the pronotum, occiput with a hardly perceptible longitudinal arcuation; interocular region but little narrower than the greatest width of the fastigium; rostrum very long and deep, occupying nearly half the length of the head and the greater part of the depth; outline when seen from the side with fastigium slightly ascending from the interocular region, face nearly horizontal, inter-antennal portion rounded to the acute angulate fronto-fastigial angle; fastigium lanceolate, the greatest width contained twice (♂) or more than twice (♀) in the length, apex very narrowly rounded, lateral margins distinctly carinate, surface tectate, median carina as distinct as the lateral and extending to the inter-antennal region; lateral foveolæ very elongate, lanceolate; frontal costa narrow, very slightly but regularly expanding ventrad in the male, very narrow dorsad, expanding somewhat in the inter-antennal region and subequal ventrad in the female, in both sexes moderately sulcate and becoming obsolete before reaching the clypeal margin; eyes flattened, elongate ovate, not at all prominent; antennæ, in the male at least, slightly exceeding the head and entire thorax in length, thick, three-sided, one narrower than the others, ensiform. Pronotum about twice as long as its width, cephalic margin of dorsum truncato-rotundate, caudal margin truncate, median carina distinct; lateral lobes with the ventral margin truncate. Wings and tegmina undeveloped. Prosternum with a very distinct longitudinal rounded tubercle; mesosternal foramina considerably impressed. Abdomen with the segments considerably elongate; supra-anal plate in both sexes strongly produced, needle-like, its length being but very slightly less than the dorsal length of the pronotum; cerci somewhat compressed, simple, sub-styliform; subgenital plate of male produced into a compressed, slightly arcuate knife-like structure, slightly more than half again as long as the supra-anal plate; ovi-

positor jaws of the female placed well under the projecting supra-anal plate. Cephalic and median limbs very small; caudal femora reaching to the fifth abdominal segment, very slender, tapering; caudal tibiæ equal to the femora in length, armed on the external margin with fourteen to sixteen small spines.

General colors of female burnt carmine and apple green, the venter of the body and head ochraceous, the carmine strongest on the dorsum, the green only on the limbs; caudal femora yellowish proximad. Color of male destroyed by immersion in liquid preservative.

MEASUREMENTS.

	Male.	*Female.*
Length of body (including subgenital and supra-anal plates)	31.0 mm.	44.0 mm.
Length of head	5.5	7.2
Length of fastigium	2.7	3.8
Length of pronotum	3.2	5.0
Length of caudal femur	10.5	13.6
Length of supra-anal plate	3.4	4.4
Length of subgenital plate	5.0	

A single pair have been examined. Doctor McClung, of the University of Kansas, who has studied the spermatogenesis of this species and whose assistants collected specimens under Professor Snow, informs me that "specimens such as those you have were constantly caught *in copulo*, and a microscopical examination of the testes shows the spermatozoa well developed." The specimens in hand have the tegmina and wing pads in the reversed nymphal condition.

Eritettix variabilis (Bruner).

Santa Rita mountains, 5000 to 8000 feet, June and July. 1907. F. H. Snow. One male, four females.

One of the females in this series is in a greenish phase of coloration, while two of the remaining females have a pattern of chiefly solid contrasting colors. The green phase has the greater part of the head, dorsal half of the lateral lobes of the pronotum, the pale stripe on the tegmina and the dorsal face of the caudal femora apple green, while the strongly contrasted phase has broad seal brown postocular bars extending over the head and pronotum and regularly expanding in width, the dorsal aspect much lighter, either ochraceous or rust red, and the usual dark portions of the tegmina also seal brown. The supplementary carinæ of the pronotum are distinctly but not strongly indicated in two of the females, represented by the

merest traces in the female and completely absent in the two contrasting colored females.

The only previous Arizona record of this species is from Douglas, Cochise county.

Amphitornus ornatus McNeill.

Santa Rita mountains, 5000 to 8000 feet, June and July, 1907. F. H. Snow. One male, one female.

Cordillacris pima Rehn.

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male.

This species was known only from the Baboquivari mountains, Pima county, Arizona.

Psolœssa texana Scudder.

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One female.

This specimen is in the blackish phase of coloration—the typical *texana* form.

Aulocara femoratum Scudder.

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male.

This species is now known in Arizona from the Huachuca and Santa Rita mountains, and from Phœnix.

Arphia aberrans Bruner.

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male, one female.

This species is now known from localities extending from the Huachuca range to Nogales, Ariz.

Hippiscus corallipes (Haldeman).

Santa Rita mountains, 5000 to 8000 feet, June and July, 1907. F. H. Snow. One male, one female.

Scirtetica ritensis, n. sp. (Plate 63.)

Type: ♀ ; Santa Rita mountains, Pima and Santa Cruz counties, Arizona. Elevation, 5000 to 8000 feet. July, 1907. F. H. Snow. (University of Kansas.)

A very beautiful species of the genus, differing from its allies in the absence of a median band on the wings, the dark color being on the periphery, in the color of the disk and in the heavy, robust build.

Size medium; form robust. Head with the extreme width very slightly greater than the greatest width of the cephalic

margin of the pronotum; occiput slightly arcuate longitudinally, the caudal section of vertex with a pair of distinctly impressed subpyriform areas; interocular region slightly wider than the fastigium, broadly and deeply sulcate; fastigium very greatly declivent, sulcate as in the interocular space, the sulcate portion, however, being slightly broader than between the eyes; frontal costa somewhat narrower than the fastigium dorsad, very gradually expanding ventrad to very near the clypeal suture, where the margins curve strongly laterad, sulcate ventrad to immediately dorsad of the ocellus, where the sulcus terminates abruptly, and from the ocellus ventrad it is present shallower and sub-obsolete as the clypeal suture is approached; lateral foveolæ lanceolate, trigonal, distinctly impressed; eyes broad, somewhat depressed ovoid in outline, about equal in length to the infra-ocular groove, moderately prominent when viewed from the dorsum; antennæ about equal to the dorsal length of the head and pronotum; ventral portion of head distinctly broader than the dorsal. Pronotum with the length of the disk about half again the dorsal length of the head, and with the greatest width of the disk but slightly shorter than the length; cephalic dorsal margin very slightly obtuse-angulate, caudal margin decidedly obtuse-angulate; lateral angles of the disk very distinct on the metazona and the cephalic portion of the prozona, broken and sub-obsolete mesad; median carina distinct, moderately elevated, straight, cut by the transverse sulcus very slightly cephalad of the middle; lateral lobes distinctly deeper than long, the cephalic and caudal margins obliquely emarginato-sinuate, ventro-caudal angle broadly rounded. Tegmina exceeding the tips of the caudal femora by slightly more than the length of the pronotum, moderately broad, slightly narrowing distad, the apex obliquely rotundato-truncate; intercalary vein prominent, through the greater part of its length closer to the median than to the ulnar vein. Wing with the greatest width contained one and one-thirds times in the length, apex sub-rectangulate with the distal portion of the costal margin arcuate. Mesosternal lobes with the interspace very strongly transverse; interspace between the metasternal lobes transverse. Caudal femora robust, the ventro-lateral carina distinctly lamellate, reaching its greatest expansion at two-fifths the distance from the apex, pattern of the paginæ distinct; caudal tibiæ slightly shorter than the femora, armed laterad with seven spines.

General colors vandyke brown and pea green, marbled and

blotched one over the other, the tegmina, dorsal face of the caudal femora and disk of the pronotum with the green predominating; ventral surface isabella color. Dorsum of the head and pronotum with a regular figure of green which is margined laterad with clove brown, this figure being constricted at the caudal margin of the head and almost severed mesad on the pronotum; antennæ clove brown annulate with pea green, their insertion bordered dorsad and ventrad by a pair of transverse lines of clove brown; eye walnut brown. Wings with the disk orange rufous, the distal and caudal margins with a moderately broad band of vandyke brown which fails to reach the proximal margin, ulnar tænia extending about half way to the base of the wing; apex with the smaller areas and a few of the short veins creamy white. Caudal femora with the dorsal face crossed by a median and a distomedian bar of clove brown, while the apex is touched with the same color, ventral sulcus washed with pale blue; caudal tibiæ turquoise blue with the lateral face of the proximal third greenish white and the extreme distal portion of the internal face blackish, leaving a pregenicular pale annulus, the apex dark blue, and a dark blue annulus placed next to the pale one; tarsal joints very pale ochraceous.

MEASUREMENTS.

Length of body	23.8 mm.
Length of pronotum	4.5
Length of caudal femur	12.0
Length of tegmen	21.0

The type specimen is the only one seen by the author.

Tomonotus aztecus (Saussure).

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male.

Mestobregma rubripenne (Bruner).

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male, one female.

Conozoa carinata Rehn.

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One female.

Trimerotropis alliciens (Scudder).

Santa Rita mountains, 5000 to 8000 feet, June and July, 1907. F. H. Snow. Three males.

These specimens are somewhat smaller than a female from the Huachuca mountains.

Trimerotropis laticincta (Saussure).

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male, one female.

This species has previously been recorded from Nogales, Douglas and the Huachuca mountains in southern Arizona, and Flagstaff in northern Arizona.

Trimerotropis cyaneipennis (Bruner).

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One female.

Heliastus benjamini Caudell.

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One female.

This specimen has pale interrupted decussate markings on the pronotum.

Previous records of this species are from the Huachuca mountains, the Baboquivari mountains, and Nogales, Ariz.

Heliastus aridus (Bruner).

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male.

Dactylotum variegatum (Scudder).

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. Two females.

TETTIGONIDÆ.

Arethæa sellata Rehn.

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male.

This is the first record of the species outside of the Huachuca mountains.

Scudderia furcifera (Scudder).

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male.

GRYLLIDÆ.

Gryllus alogus Rehn.

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. Two females.

These specimens measure as follows:

Length of Pronotum.	*Tegmen.*	*Caudal femur.*	*Ovipositor.*
4.0 mm.	9.0 mm.	12 mm.	14.5 mm.
3.3	5.5	11	13.8

This species has been recorded from the Huachuca mountains and Phœnix, in addition to Albuquerque, the type locality.

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OBSERVATIONS ON THE GRYLLIDÆ: III. NOTES ON THE CLASSIFICATION AND ON SOME HABITS OF CERTAIN CRICKETS, *W. J. Baumgartner.*

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OBSERVATIONS ON THE GRYLLIDÆ: III. NOTES ON THE CLASSIFICATION AND ON SOME HABITS OF CERTAIN CRICKETS.

BY W. J. BAUMGARTNER.
(Contribution from the Zoölogical Laboratory, No. 195.)

CLASSIFICATION.

IN the course of collecting material for some cytological studies on the crickets, I was early confronted with the question of what are the true species of *Gryllus*. The first specimens collected I (*2*) called *Gryllus assimilis*, after carefully comparing them with the labeled specimens in the University of Kansas collection, and after reading such descriptions as were then available in the library. Later I collected about Chicago, Ill., and Woods Hole, Mass. My attempts at classifying these specimens led me to the conclusion that the species of *Gryllus*, the common larger field crickets, are not fixed but grade into each other. I found that in all of these places there were two groups with different breeding seasons—one that passed the winter in the nymph stage, and another that passed it in the egg. The former matures and breeds around Lawrance, Kan., during June and early July, and the other during the latter part of August and September.

This question of the true species in *Gryllus* was frequently discussed with my fellow student, Dr. F. E. Lutz, now of Cold Spring Harbor, N. Y., during our study at the University of Chicago. I am glad to confirm his recent publication (*14*) in which he says that the species of *Gryllus* as now named do not differ in characters, "but merely in the degree of common characters." My study has not been especially along the line

of taxonomic characters; but my attempts at classifying the specimens collected in Douglas and Harvey counties, Kansas, in Chicago, Ill., in Woods Hole, Mass., in the Santa Rita mountains, Arizona, and in Tarpon, Tex., trying to follow the keys given by Scudder, Blatchley, De Saussure and others, have led me to believe that Lutz is right when he says: "Either we simply name stages in a great continuous mass of variation and call them species or there is but one species of *Gryllus* in eastern United States, and the names we give are not the names of species at all, but simply inaccurate, shorthand expressions for recording the approximate size, proportions and color of individuals found." This applies to our common field crickets; and I do not think that it should be limited to the eastern United States, but should include the central portion as well.

On a collecting trip to Tarpon, Tex., last summer, I found a color variation which confirms this opinion that all these so-called species grade into each other. On the low sandy islands I found that the crickets were *straw yellow*. Most of them were in the last or next to the last nymph stage. This was about June 12. At first I thought they were the imported *Gryllus domesticus;* but later collecting disclosed some with a few, and some with many dark markings. A few of the adults taken subsequently were quite black. These were under the same boards or stones with the straw-colored ones, and were mating with them; and they probably came from the same mother. A number of nymphs were brought to the laboratory at Lawrence and raised to maturity. All of them turned much darker and some became jet black. As far as I could see these black ones could not be distinguished from our native species.

One peculiarity of these crickets on the islands at Tarpon offered an additional reason for thinking they were *G. domesticus,* or a closely allied species; *i. e.,* the young nymphs varied much in their stages of development, a peculiarity I had noticed in the domestic species in the greenhouses in Chicago. This fact must be due to the climatic conditions—both forms developing where there is a long-continued breeding season, with even temperature.

In the laboratory I found that these Texas forms mated very readily with our Kansas forms, both the spring-maturing and autumn-maturing broods. Some of the adults I brought with me paired with some tardy spring forms and some of the

smallest nymphs were not matured before autumn adults appeared.

In trying to classify these southern forms I finally concluded that they were our common black field crickets, which had lost *a little, very much,* or *nearly all* of their pigment. Although Blatchley, Scudder, and De Saussure use the color difference as one of the prominent characters separating species, I do not believe that it can properly be so used. "Black color" and "straw color" do not stand for different species in the crickets of the Texas coast. The black gradually shades off into the straw color; and a black one and a light one may have the same mother.

An examination of the germ cells reveals no differences in cell structure between the southern light-colored specimens and our native black ones. But both differ markedly from that found in *Gryllus domesticus,* as has been and will be shown by the papers dealing with spermatogenesis.

All of the collections made in the various localities show dimorphism as to wing length. The short-winged forms are very much more numerous in all places, but the long-winged forms vary greatly in frequency in the several localities, as Lutz (*14*) has found.

Blatchley (*6*) is correct when he suggests that the failure of past monographers of this genus is in part due to the fact that they have neglected the study of the animals in the field. By using this method he has added some very useful hints on the habits and structure, as they bear on the classification. He has plainly shown that there are in many localities really two broods, one maturing early and the other later. He considers them as belonging to different species. Lutz denies this. In whatever region I have observed the two broods, the autumn specimens are larger and more robust than the earlier ones. They also differ in proportions and color enough to represent two species according to ordinary criteria for species; but the intergrading of the forms from different localities would remove all distinctive characteristics. So while Blatchley is apparently right, I feel confident that extensive careful collecting will show that Lutz is correct.

The earlier brood lives "in burrows singly or in pairs," while the later ones "are more sociable," and there is not much "forsaking of burrows," as Blatchley (*6*) thinks. My observations have led me to the following conclusions: Of the

spring brood each individual has a separate well-made burrow, early in the season, usually under some stone or board. The male keeps his as long as he lives, or well through the breeding period at least; while the female abandons hers when she becomes an adult, or even before. Thereafter she may be found with the male in his burrow or in any convenient hiding place.

The young individuals of the autumn brood never make much of a burrow, but live under bunches of loose, dry grass or old rags, or whatever they find. I have frequently found more than a dozen in an old newspaper in the grass. The adult males sometimes have a sort of burrow, particularly late in the season, but most of the time I find them in any kind of a hiding place. I am quite sure, however, that these creatures, young and old, especially the males, have a selected spot in the grass or paper, which serves as their home, and so the difference between the spring and autumn forms is really this: the former dig a burrow for a home, while the latter simply select some convenient place to stay.

Judging from my study of the germ cells of *Gryllus domesticus,* given in a former paper (*3*), this species is quite different from the other forms. The difference of chromosome number and shape are such that I should expect the domestic species to be very different in taxonomic characters; but such is not the case.

In other genera of the family Gryllidæ the species are more distinct and limited. In *Œcanthus,* following Hart (*10*), we classify the species largely by the color markings on the basal joints of the antennæ, and this seems to be quite constant. I have found that I can separate the nymphs quite readily by means of these markings. *Nemobius* shows more variation, and probably after large, widespread collecting the species may prove to intergrade. In *Gryllotalpa* the species are quite distinct.

FOOD HABITS.

Very many observers have written of the food habits. It is known that the common black field crickets may eat almost anything. In captivity they will sometimes devour each other, the stronger ones feasting on the weaker ones even before they are dead. I have seen a female chew the wing of a male, and I have found a crippled female with her abdomen partly eaten away. In their free life I think this rarely or never occurs.

The females will eat the empty spermatophores whenever they find them.

Among the mole crickets I observed this peculiarity between two species. In a box of specimens of *Scapteriscus* sent me from Porto Rico I never discovered any partially devoured ones among the few dead specimens; but while collecting our own species *Gryllotalpa borealis,* in northern Indiana, I placed one female adult and six nymphs in a bottle full of sand in the field. When I returned to the laboratory I found but two nymphs, the others having been devoured by the adult. This, with some later experiences, led me to believe that adults will eat the nymphs whenever they find them in their burrowings. However, this cannot be true for the very young nymphs, as the eggs are laid in a mass in a much frequented part of the burrow, and the mother, no doubt, cares for the eggs and young for a while.

EGG-LAYING.

Blatchley (*6*) says: "The eggs of most crickets are laid singly in the ground." My observations confirm this as far as *Gryllus* and *Nemobius* are concerned. The large black field cricket selects usually a somewhat barren spot in a grassy field, where she lays her eggs. She will force her ovipositor into the ground and deposit a single egg, then removing the ovipositor partly will put it down at a different angle and plant another egg, and repeating the process will leave a third. On no occasion did I see more than four eggs laid without the ovipositor being completely removed and pushed into the ground at a new place. *Nemobius* lays its eggs in a similar manner. Two or three, rarely four, eggs are laid almost side by side, and then the next batch are placed a quarter of an inch or more away.

In but one instance did I find eggs laid by the mole cricket. They were "in a heap on the floor in the enlarged part of a side gallery," just as Barrett (*1*) has described.

CHIRPING.

A peculiar habit of the mole crickets, of which I made brief mention in an abstract (*4*), is the *chirping of the female.* A hurried examination of the tegmina of the females will show that the nerves are modified into a rasping and sounding organ, which is not as large or as well developed as that of the male, but well enough to have made thoughtful observers of the past

suspect that it might function, and that female *Gryllotalpa* might chirp. As far as I have been able to read the literature no one has observed that they actually do so. Most of our books say that only the males stridulate. LaCordiare (*12*) says, "The chirping organs of the crickets are simple and limited to the males." Scudder, speaking of the crickets, says, "his egotistic love song." Comstock (*7*) writes, "the males of the crickets have musical organs." Lang (*13*) says: "In the Locustidæ and Gryllidæ only the males stridulate, by rubbing the rough basal portions of their wing cases against each other." Packard (*15*), after speaking of the organs in the males, says: "The females are not invariably dumb, both sexes of the European *Ephippigera* being able to faintly stridulate." Henneguy (*11*), in speaking of the musical organs, writes: "Where they are found they are well developed in the males only; in the females they are more or less rudimentary. Such is the case in the Gryllidæ." Barrett (*1*) describes the stridulating organ in the male "Changa" or Porto Rican mole cricket, *Scapteriscus didactylus;* but he has completely overlooked the same but less well developed organ in the female.

The female mole cricket has quite a loud and distinct chirp. It usually consists of a single note; but there may be several at short intervals. This note is less shrill than the ordinary call of the male. However, the male has a note very similar to that of the female which it uses for the same purposes, namely, as a means of recognition in the dark burrows. The call is always given when one individual is approaching another, especially when digging a new tunnel. Both genera, *Gryllotalpa* and *Scapteriscus,* have the stridulating organ on the female elytra, and so both must be able to chirp. I never isolated a Porto Rican female to hear its chirp, but after hearing the call of our native cricket I feel sure that I have heard the insular female's chirp also.

This unusual ability possessed by the female is an adaptation to life in underground burrows. It enables the individuals to recognize others which are approaching under conditions where sight cannot be used. Thus enemies and friends can be distinguished; while if the female were dumb, as she is in all other crickets as far as I know, they might often attack even their mates.

PROTECTIVE GLANDS IN THE MOLE CRICKETS.

As indicated in an abstract (*4*), I have found that the correct interpretation of the function of the anal gland, which has so long puzzled investigators, is protective. Leon Dufour (*8*), a careful French investigator, first described in the mole crickets in both sexes a pair of azure or skim-milk colored glands connected with the rectum. Their secretion he compares in consistency with the vitreous humor of the human eye. To this secretion is added some excrement from the rectum, and when this mixture is expelled it forms a brown liquid of nauseating fetidity. He calls the gland "an organ of excremental secretion."

Berlese (*5*) describes the same structure and thinks it is a prostatic gland analogous to that found in the locustids. Although he found it in the female also, he does not seem to try to explain it there.

Fenard quotes both of the above descriptions and adds a good many observations of his own. He describes the gland from sections and gives the action of certain fixatives and stains upon the tissues of the gland and its contents. He states in detail the macroscopic and microscopic structure. He concludes as follows: "Judging from the position of this organ, from the consistency of the liquid which it contains, and from its points of similarity with the prostatic glands of the locustids, I think that it ought to be considered also as a gland furnishing a mucus destined to lubricate the copulating apparatus. This organ exists in the female, it is true, but in this case it furnishes without doubt still a lubricant for the vagina, or a liquid to form the nest of these insects." After describing the details of this gland in the female he says: "I think that these organs can only be some secreting agent of a mucus destined to lubricate the genital organs; or perhaps they glue together and hold the spermatophores; or perhaps again they secrete the substance used to form the nests in which are found, as we all know, two to three hundred eggs all massed together and more or less united." It is evident from this uncertainty that Fenard did not know the function of the glands in question, yet he was inclined to follow Berlese and called them "prostatic glands."

Packard, in his work on Entomology, places the anal odoriferous glands described by Dufour among the repugnatorial

glands, apparently because he has concluded that all fetid and anal glands are repulsive.

As far as the position, size and structure of these glands are concerned, these earlier observers are on the whole correct. They agree, too, in the main points. Dufour has the glands attached to the rectum, while Fenard has them attached to the genital duct. The explanation of this difference of observation is partially suggested by Fenard, when he says: "En somme ces organes paraissent d'eboucher dans une sorte de cloaque ou arrive l'oviducte." The mole crickets have but a single opening at the posterior end of the abdomen; and a short common duct carries the genital and excrementary products. This should very properly be called a "cloaca." Into this cavity the short ducts of the anal glands empty.

Fenard gives as the sizes of the glands "about six millimeters in length and three millimeters in thickness." I found none as large as that, but the size would depend in part upon the amount of secretion in the gland. Both Dufour and Fenard speak of two lobes and a median constriction. There is some tendency for such a constriction to show, but it is not constant. The shape and position of the organ would depend somewhat on the amount of extension of the abdomen and the fullness of the rectum. The two lobes when present do not differ in histological structure, and not in function, as Fenard has shown by his careful work by means of sections. The walls are resistant, the cavity large, and the contents appear homogeneous, granular, and they coagulate as a result of fixation, and color strongly whenever stained. All these facts Fenard has correctly described.

But Fenard must have worked with preserved specimens only, or he would not have made the error concerning the function of the gland. Although he quotes Dufour, he cannot have followed his suggestion when the latter says: "If one seizes a mole cricket of either sex, it squirts from the anus a brown liquid of nauseating fetidity. This liquid is formed in part by excrement from the rectum and is in part the product of a special secretion."

I have studied *Scapteriscus didactylus* from Porto Rico and *Gryllotalpa borealis* taken in northern Indiana and in eastern Kansas. My observations and experiments show that the above quotation is correct in most parts. If the insect is held or irritated in the region of the head or thorax, there is no discharge.

But if held or pinched or pricked or chemically irritated on any side of the posterior part of the abdomen, or on the hind legs, there is always ejected from the anus a bluish-white liquid with some excrement. The discharge is directed as nearly as possible to the point of attack, be it above, below, behind, or on either side of the abdomen. It is driven with considerable force, enough in some instances to carry it across an aquarium eight inches in diameter. After several ejections there is less excrement in the liquid, which becomes almost colorless, losing its milkiness.

The ejected mass has a very fetid odor and is *very sticky,* so sticky that a half-grown nymph can readily be suspended by lightly touching a needle to some of the secretion and then to its abdomen. An adult female, in spite of her strong legs, was held for nearly a minute as a result of touching her besmeared body against the side of the jar.

In some breeding experiments reported elsewhere I was able to study the effect of this ejection and the conditions under which it is made. There was no discharge when the male was carefully introduced into the jar with the female, but on one occasion it happened that the male became excited and rushed upon the female in his attempt to get away. He received a discharge upon his head and into his face. He stood for a long time trying to clean this off. He apparently could remove but little of it, and died on the second day thereafter. At another time a female received a lesser discharge from a male. She, too, spent hours trying to scrape off the sticky stuff, but failed, and died on the third day. The other pair lived for many weeks longer. Perfectly calm individuals, when put into a jar in which there had been a discharge a day or so before, became very much agitated and tried hard to escape from the enclosure. This behavior suggests that when these insects get this odor it warns them that an enemy has been or is near, and they try to escape. I repeated this test several times with the same result. I introduced some affected sand into a jar containing a calm individual. He became agitated. In every instance the crickets became excited when they perceived the odor.

The fetidity of the liquid must repel very ardent pursuers, and the stickiness must retard them should they become entangled in a discharge. It is, no doubt, for the purpose of so entangling the enemy that the cricket directs its discharge toward the point of attack.

This defensive organ probably explains the fact that mole crickets have so few natural enemies, as reported by Barrett (*1*).

Since the Gryllotalpidæ move most of the time in underground burrows the discharge from the anus would protect against attacks from the rear. Hence there is no discharge when the irritation is on the anterior half of the body. The head and thorax, besides being very hard, are further protected by the powerful fore legs. The abdomen is comparatively soft and without other protection than that described above.

My observations and experiments prove conclusively that the secretion of the anal glands, or "prostatic glands" of Berlese and Fenard, is preëminently protective, as any one who will take the trouble to secure a live specimen and repeat these tests can see for himself. Neither Berlese nor Fenard can have handled live individuals, or they should have seen the use of the anal secretion.

As far as we know no other orthopteran has these protective glands, nor has it the same peculiar habits. The mole crickets running along the narrow underground tunnels have the soft abdomens constantly exposed to the attacks of enemies which they cannot see or perceive, so they have developed a special organ which can instantly repel or retard a pursuer.

SUMMARY.

1. The species of *Gryllus* in eastern and central United States are not distinct, but form one large intergrading series, as Lutz has shown. This is true also for the supposed distinguishing *straw* and *dark* colors as shown by the specimens collected in Texas.

2. The female mole cricket has a partially developed chirping organ on its elytra. With this instrument it produces a single note used as means of recognition in the dark tunnels.

3. The anal gland of Dufour, the prostatic gland of Berlese and Fenard, is protective in function. The secretion operates as a repellant by its fetidity, and as a retardant by its stickiness.

4. Both the female musical organ and the protective gland are adaptations to life in underground tunnels.

UNIVERSITY OF KANSAS,
May 10, 1909.

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CONTENTS:

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OBSERVATIONS ON THE GRYLLIDÆ: IV. COPULATION.

BY W. J. BAUMGARTNER.

(Contribution from the Zoölogical Laboratory, No. 196.)

Plate LXIV.

HISTORICAL NOTE.

THE first suggestion of the correct method of the transfer of the spermatozoa from the male to the female in the Gryllidæ is given by Siebold (*20*), who described the glands annexed to the ejaculatory duct and noted that their secretion coagulated very readily when exposed to the air, and that it probably served to fill and distend the copulatory pouch just as it filled and distended the penis. The latter organ surrounded a portion of the sperm and thus formed the spermatophore. Siebold believed with the older naturalists that the spermatophore is the end of the penis broken off and often reformed.

Stein (*22*) by his careful investigations gave the correct idea of the spermatophore as a vesicle formed by the secretion of the annexed glands and used to carry the sperm. Siebold (*21*) accepted this correction and later defended it. But he studied mostly locustids, and so we do not know that this part of his notes concerned the gryllids; however, some of his work was done on *Gryllus*, and so the work must be mentioned in a review of the subject.

We do have a comparatively detailed description of the act or acts of copulation in the crickets as early as 1855 by a Frenchman, M. Charles Lespes (*11*). But the work was little known and then questioned by Milne-Edwards (*15*); so that

textbooks of to-day still disregard it, or quote it with a question mark. Since I shall use Lespes's work very freely in my own description, I shall not review it farther here. Suffice it to say that the observations are strikingly keen and correct for having been made so early, and they should long since have been inserted in our texts.

Leydig (*13*) in his fine work, dealing more with the histological side of the subject, says that in many invertebrates the accessory sex glands form a spermatophore.

Milne-Edwards (*15*), in 1870, said, speaking of the spermatophore mentioned by Stein and Siebold: "It is possible that it may exist in certain cases, but in other cases it is evident to me that the appendage in question was certainly a part of the penis." Of Lespes's statements he writes: "It does not seem to me sufficiently demonstrated that the so-called spermatophore is not the terminal part of the penis which in copulation is broken off and remains inserted in the female apparatus, as it does so often in the case of other insects."

Milne-Edwards's prominent position, no doubt, gave his work the preponderance, and so we find Lespes's work hardly ever quoted. To show how it was disregarded, let me quote from Girard, who wrote three large volumes on entomology. In 1873 (*7*) he said of the glands joined to the *vas deferens,* "They pour in a liquid to delay or modify the sperm." In the third volume, in 1885 (*8*), he repeated the above statement about delaying the sperm, and then adds, "or perhaps to give more activity to the sperm, which are almost immotile in the testis."

Berlese (*4*) studied the external and internal genital organs of various orthopteran species. In the body of his work he does not seem to realize that the Gryllidæ differ from the other Orthoptera, and so he describes in *Gryllus* a penis and all the other accessory parts, without any thought of their correct function. In an appended "Physiological Note" he comes nearer the truth. He says, concerning copulation, that fertilization is internal and that copulation in the Acrididæ and perhaps in the Mantidæ is by means of a penis, the act lasting a relatively long time; while in the Locustidæ and Gryllidæ, "the male mounts on the back of the female, the penis being inserted in the vagina and the sperm injected in a short time."

He supposes that the mucus secretion of the annexed glands serves to lubricate the organs. He notes the fact that in *Gryllus* and *Gryllotalpa* the mucous secretion flows out through the same duct with the sperm. He adds further: "In *Gryllus*, I think, fecundation is more complex, occurring by means of a special organ which is left in the vagina of the female and which can be reformed up to three times a day, as I myself have seen. This singular organ holds the sperm in its interior and is a true spermatophore." The only way I can explain how Berlese came to overlook the discrepancy between his description and his "Physiological Note" is to think that in the body of the paper he was concerned with the homology of the parts in the various groups of Orthoptera, and so did not think of the function.

Graber (*9*) shows that in many Orthoptera there is no true copulation, but that the sperm are transferred by spermatophores. Palmen (*17*) studied by means of dissection and sections several species of Orthoptera, and he confirms Graber, showing the absence of a penis and the correct method of spermatozoon transfer.

Peytoureau (*19*) in his long thesis on the "Morphology of the Genital Armature of Insects," does not even mention Lespes's work, again showing how little this early, accurate investigation is known; or if known, how little it is appreciated. Peytoureau worked on the mole crickets, some long-horned and some short-horned grasshoppers. His special study was the hard parts, and he showed that the penis is absent, except in the Acrididæ, the Forficulidæ and the Ephemeridæ. But his study was centered about the homology of the male and female hard parts. Questions of the number of abdominal segments, the relative position of the ovipositor and the penis and to what segments these belonged, were the ones which he considered; and so the only observation of importance bearing upon our topic is the absence of the penis in the Gryllidæ.

Fenard (*6*) in 1896 published a long paper on "Les Organes Complimentaries Internes de L'appariel Genital des Orthoptères." He studied both sections and dissections of the annexed glands in the two sexes of several genera of most of the families of Orthoptera. In his observations he is correct on the whole. But in his interpretations he is not always so fortunate. The errors made are due largely to the fact, I

think, that he worked with preserved specimens only, and so missed the function of parts as proven by the habits of the animals. The suggestion that the anal gland in the mole crickets secretes a lubricant for the genital organs is entirely wrong, as I have shown elsewhere (*2*). Concerning the glands annexed to the ejaculatory duct he reasons correctly, as follows: Gryllids and locustids form a spermatophore, as shown by Siebold (*21*), Lespes (*11*) and Berlese (*4*). But these families are the ones that have this mass of annexed glands; hence these glands secrete the substance for the spermatophore. He thinks there must be a spermatophore formed in *Gryllotalpa*, although it has never been seen because of the habits of these insects. In this surmising he was fortunate, as I show below. But he is mistaken in the function of what he calls the ear-shaped gland. He thinks that it is analogous to the anal gland of *Gryllotalpa*. This is surely wrong. The position of the pair of glands and its relation to the excretory duct is such that it can have no such function as I have found for the anal glands of the mole crickets. My many dissections and observations lead me to believe that there is no gland which secretes a lubricant for the sexual organs.

Although the method of copulation by spermatophore and the function of the annexed glands have been so well described, it is rather disappointing to see our textbooks still quoting Carus's figures showing that the male generative apparatus of *Gryllus* is among the simplest found in the insects. See Henneguy (*10*) *et al.* Although this Frenchman cites Fenard's paper in his bibliography, he makes no reference to his findings, but says of the annexed glands: "Elles ont été peu étudiés jusqu' icé." But under the topic of "Copulation" he gives the process in *Gryllus* in detail, quoting Lespes's description and some of his figures of the spermatophore. In this case he does better than our own Packard (*18*), who, in speaking of the spermatophore, says: "In *Locusta*, and perhaps also in *Gryllus*, the sperm is enveloped by the secretion of the accessory glands of the seminal duct." This "perhaps" is very striking when one considers how easy it is for any one to observe copulation in our common field cricket. One need only catch an individual of each sex during the height of the breeding season, as indicated by their great chorus of chirping, and place them with a little grass over night or longer into

separate jars. Then slowly turn the glass with the male over that with the female. In a comparatively short time the male will begin his chirping and one can see the whole series of acts of courting and copulation. After observing the process one can hardly prevent a smile when he reads Loeb's (*14*) quotation of Yersin's experiment of having a pair of decapitated crickets copulate, and then see the admonition: "Of course it was necessary to place the male *on* the female." One would hope that the observations in the experiment itself, and any conclusions drawn therefrom, may be more to the point than is the self-evident suggestion added at the end.

DESCRIPTION.

A free translation of Lespes's paper of 1855 would describe fairly correctly and with a good deal of detail the various steps in the process of copulation. He notes at the beginning that there is no true copulation, but that the male simply deposits a spermatophore into the posterior end of the abdomen of the female; and that this process may be repeated many times.

The Courting.

Lespes (*11*) studied first the field cricket. Catching specimens of both sexes, he got them accustomed to their new surroundings and then brought the two together. "The male soon began to chirp, and to move around the female. Approaching nearer and continuing his chirping he turned his abdomen, carried very low, toward the head of the female. She remained quiet for ten minutes, not appearing to notice the maneuvers of her mate; then she moved forward a little and began to caress his abdomen with her mouth parts. Presently she mounted partly on his back; and he, stopping the chirping, glided back under her. The female vulva now rested above the end of the male abdomen."

This description of the courting is fairly exact. The caressing by the female is not essential or even usual. Sometimes the female hardly stops feeding during the whole process, simply allowing the male to slide under her. When the male approaches the female, or when she approaches him, his chirp becomes much softer and less shrill. On some occasions if the female did not yield after a certain amount of chirping the male became angry and fought his mate.

The Transfer of the Spermatophore.

Lespes says: "The plate, the tenth tergite, which covers the opening of the anus and the pieces of the genital armature, was raised, and a hook of this apparatus penetrated into the vulva. Immediately after this the end of a small brown body directed by the hook was introduced into this opening. The female then left the male, carrying the small brown body of which I have spoken." Lespes then removed the small apparatus from the female quite easily, as only its front end was inserted in the vulva. This apparatus he found composed of a small hard ampulla and a thin, transparent plate curiously twisted. Upon examining a jar in which he kept a male over night he discovered that there was a spermatophore lying on the bottom. He later proved that this was not exceptional, but that males deprived of females rid themselves of their spermatophores.

The male which had copulated with the female seemed exhausted and did not renew his courting for several hours, although he was again put in with the female. Lespes observed the transfer of the spermatophore very often, and each time he got a spermatophore from the female, which he studied later.

Taking up this transfer in detail, the Frenchman describes the position of the spermatophore in the male. "It lies in the posterior end of the abdomen covered by the supra-anal plate. To see it *in situ*, gently raise the anal plate which covers the anus; below this there is a horny plate with three hooks projecting backwards and upwards, and below this there is the spermatophore lying in the concavity of the eighth sternite. The ampulla extends backwards and is supported on either side by fleshy pallets (plate is used by Lespes). The plate and the thread of the apparatus are still in the organs which formed them. At the moment of copulation the supra-anal plate is raised and the hooks are introduced into the vulva, holding the two individuals firmly together. The end of the spermatophore plate from which projects the thread glides in a kind of hollow groove in behind the hook in a manner analogous to that which surgeons use when they introduce a bistoury upon a groove-director. By a rapid movement from before backwards the plate is fastened and the two pallets which hold the ampulla move aside, and so the spermatophore is carried by the

female, held by the plate only. Ten minutes after copulation some males had formed a new spermatophore, but it was soft and white, and attained its hardness and color only after an hour. The spermatophore can be quite readily removed from the male by means of a forceps. To form a new spermatophore the male goes through some motions similar to those used in defecation. The female carries the spermatophore for some time, in one case six hours, and it was not dropped until she mounted a male again."

My own observations show that this account is quite correct in most of the details. Our common black field cricket differs in the following points: The female if undisturbed will not leave the male immediately after the placing of the spermatophore. She may remain perfectly quiet for several minutes.

A third element of this sperm-bearer, which Lespes seems to consider of little importance, is very essential, as I shall prove below. It is the thread which projects beyond the plate. (See fig. I.) This thread slides in the groove when the apparatus is being introduced. The mechanical process can be better understood by examining figure 5. The ampulla lies between the two pallets, which are then extended backward very far. The plate lies in the anterior part of the mold and the thread lies in the groove below the hooks. In transferring the spermatophore the male turns the hooks upward by swinging them, or rather the whole mold, at its attachment to the tergite as a pivot. By this turning the hooks first extend upward and then forward and are thus inserted into the vulva of the female, holding her firmly. Then by means of the muscular mass behind, the thread and plate of the spermatophore are pushed far into the vulva. The hooks of the plate hold the apparatus and the thread carries the sperm into the spermatheca. The thread and the anterior end of the plate are quite flexible, and so they are bent and directed by the "independent piece with the short stylet" which guides the thread into the duct leading to the spermatheca. The "forward and backwards" movements are concerned with the proper placing of the thread.

The time suggested for a male to copulate a second time is much too long. I have had a second pairing occur in fifteen minutes. The spermatophore in this case was whiter and softer than usual, but as far as I could see it was a normal

copulation. This intervening time was unusually short, but I am sure that it does not take an hour for a spermatophore to harden after it is formed.

I am sure that the males of *our* field crickets rid themselves of the spermatophore, if deprived of the females, only *exceptionally*. In all my many observations I have seen the thing occur but three times, twice in *Gryllus* and once in *Nemobius*. In every case it was rubbed off after an unsuccessful attempt to introduce it into the female. In these trials the plate was, no doubt, partially removed from its normal position in the forming organs, because in most cases the males made no effort to remove the spermatophore, although they had tried to copulate.

I have not seen that the males make any movements while forming a spermatophore, but I would not positively deny that they do so. I have frequently kept them under observation for a few hours after copulation; some would form a new sperm bearer and others not. One male copulated a second time after a very short interval, but I did not watch him meanwhile. Some other specimens did not have the spermatophore formed after hours of watching.

The female carries the vesicle very frequently until she is about to mate again. If this comes soon after a previous copulation, she will remove the vesicle. She does this with her mouth parts, bending the abdomen ventrally. She may place herself partly on her back and holding the abdomen against the ground force her mouth parts back so as to reach the ampulla of the spermatophore. If the abdomen is too much distended by eggs, she frequently rubs it off by dragging the abdomen on the ground. The longer a spermatophore has been carried by the female the easier it is removed. In only one instance did I see a female mount upon a male with the sperm bearer still in place. After a good many efforts the male succeeded in pushing the old spermatophore partially out of the way and placing a new one. The female then carried both, the old one apparently hanging on by one hook.

The Spermatophore.

Lespes says: "The spermatophore of the field cricket is composed of a vesicle almost round, of a brown, more or less dark, color. It terminates at one extremity by a whitish papilla and is continued on the other end by a transparent plate, al-

most quadrilateral, formed by a thin membrane stretched over three small cartilaginous pieces. One of these is median and connects directly with the vesicle. It is tubular and contains a horny thread which continues well beyond the plate. The other two, situated to the right and left, are arch shaped, and their two ends covered by the membrane, form on either side two tooth-like hooks which serve to fix the apparatus in the vagina. The size of the spermatophore varies a little but ordinarily it attains almost 4 mm. from the papilla to the end of the plate. The thread appears longer or shorter according as it projects more or less from its tube. The spermatophore is of different consistency in different parts. The vesicle is extremely solid and its walls are very thick, while the plate and its cartilaginous thread are soft at the moment of copulation; besides, it is covered by a white, thick liquid which presents to me all the characteristics of a sperm fluid. The thick, hard vesicle, composed apparently of double walls, toward the extremities is hollowed out at the center. The roundish cavity is full of sperm. At one end a blind tube projects from the cavity into the ampulla. At the other end the cavity continues as a straight canal through the whole length of the plate. This canal contains the horny thread.

"The white liquid which covers the plate when first removed from the female shows, when examined with a high magnifier, a large number of small, thread-like zoösperms. They are about .04 mm. long and .002 mm. thick. These same bodies in great number fill the cavity of the vesicle. They were never united into feather-like bundles, nor did they ever show any movement. The fluid taken from the testis of the male or the copulating pouch of the female contains many very similar zoösperms. These never exhibited movement, however treated. Put into water, some of them twisted themselves into knots.

"When the female lets the spermatophore fall the walls of the vesicle are slightly ridged, but it still contains some sperm. The horny thread is no longer found in the tube of the plate."

I have quoted the above description at length because it gives many facts as I find them in our American species.

The vesicle and the plate are similar to those described above (see figs. 1 and 2). The thread is not contained in the tube, but it is the tube itself continued, and it is much longer, and bent back so as to run parallel with the plane of the plate

and vesicle (see fig. 1). It is a hollow tube for its whole length and the sperm comes out at the *end* of the thread, and not at the end of the plate, as Lespes supposed. The thread varies in length not because "it projects more or less from the tube" but because it is broken off in removing it from the insect. Many of those that I secured at first had more or less of the end broken off. It is easier to get a spermatophore with a complete thread from the male than from the female, especially if the latter has carried the apparatus for some time. This no doubt accounts for the fact that the apparatus can be more easily removed after it has been carried for a while. When the insect drops it normally the thread has been broken off, or, more probably, partly dissolved away; but it is not entirely gone, as Lespes states.

The vesicle is apparently double-walled as the Frenchman observes (figs. 1, 2, and 3). The inner one is thicker and more granular, while the outer one is harder and quite transparent (figs. 1 and 2). It is the inner wall that continues forward and forms the thread, although this substance is less granular than that around the vesicle. The substance forming the plate is somewhat granular, and in some cases took the stain just like the inner coat of the vesicle. In the lateral parts of the plates I saw in several of my preparations many vacuoles. The thread in many of the specimens fixed and mounted in balsam shows a tendency to break away from the plate (fig. 3).

That the sperm pass out at the end of the thread was nicely shown by several specimens which I placed into a normal salt solution. The sperm flowed out very regularly and moved about for a time. In one instance it took about fifteen minutes for a vesicle to empty itself through the end of the thread. After the sperm were all out a little fluid with small granules flowed out. I do not agree with Lespes when he says that some sperm remain in the vesicle normally; nor do I think that the wrinkling is a characteristic of the empty vesicle. I could not see any difference between an empty spermatophore and a dark brown one which had been carried by a male for some time. The wrinkling, which Lespes correctly describes, is due to the longer hardening of the vesicle and does not seem to affect the cavity on the inside.

The shape of the cavity differs from that described and figured by Lespes in the total absence of the blind tube extending into the papilla. What he describes is only the second layer

of the wall of the vesicle as shown in figures 1 to 3. The dark stain here shows the outer limits of the inner lining, and the cavity is on the inside, as shown in the outline drawings. The cavity is easily visible in the preparations but the photos do not bring it out. At the posterior end the cavity is flattened and at the other end it gradually tapers down to the size of the thread; so that the shape of the opening is much like a flat-bottomed flask. In this cavity all the sperm have their heads directed toward the openings into the thread and their tails toward the papilla. Figure 11 is a small group of sperm photographed from a section of a spermatophore. In passing out of the thread the sperm manifested some movement of their own, but were not very active. Several may pass out together but only two or three heads have room side by side. The sperm are larger than Lespes thought, as can be seen by comparing with my earlier published measurements (*1*).

The Spermatophore-forming Organ.

Since many of our textbooks on entomology—see Packard (*18*) and Henneguy (*10*)—still cite *Gryllus* as showing one of the simpler conditions for the excreting ducts of the testes among the insects, I shall give a more detailed account of the male generative organs, their ducts and the accessory glands, than I should otherwise do.

The first description of these parts was given by Dufour (*5*), in *Gryllus campestris,* then by Lespes (*11*), in *G. domesticus,* later by Berlese (*4*), again in *G. campestris,* and then by Fenard (*6*), in both of the above species.

The testes lie on either side of the abdomen above the alimentary canal and extend from the second to the sixth or seventh segments. The shape is much like that of an elongated strawberry. On the outside is a thin membrane which encloses the hundreds of straight or slightly curved tubules which make up the organ (figs. 6 and 7). Their blind ends are nearly all directed more toward the posterior end of the body of the animal. At the center of the testes is a large tube, or rather an irregular sinus, which receives the openings of the hundreds of tubules (fig. 8). The small *vas deferens* leaves this sinus on the anterior ventral side and comes to the ventral side of the testes a little back of the middle. It passes backward over the tubules, and leaving them at the outer posterior edge passes back along the body wall muscles till it reaches the

ninth segment, where it passes around the cercal nerve and a few strands of muscle and ligament (figs. 7 and 8). Making a sharp bend it goes forward and ventralward. It is very much coiled upon itself from the bend on (figs. 7 and 8). The loops of the coils may lie in planes passing dorso-ventrally or laterally. The two *vasa deferentia* join and immediately empty into the posterior ventral angle of the sinus, which receives the openings of the annexed glands (fig. 9). Beginning at the cercal nerve and sometimes a little in front of the bend the duct is swollen so as to be 0.5 to 0.75 mm. in diameter (figs. 7 and 8). Fenard says there are from four to five coils and that the total length is 8 mm. In our common field cricket I found no regularity about the position or number of coils and the total length is more than 10 mm.

This swollen part of the *vas deferens* is always in the mature adult filled with a mass of sperm, all of them with their heads turned away from the testis.

Fenard (*6*), as well as the older investigators, says that "the union of the two *vasa deferentia* forms the ejaculatory duct." This is the statement generally made of the insects higher in the scale of evolution; but it is true only in a certain sense—in the sense that it serves as a common duct to carry out the secretions of the testes. First, it is not a true ejaculatory duct in the sense that it "during coition conducts the sperm into the copulatory pouch of the female"—Packard (*18*). This is true only in those insects with a penis; but in the Gryllidæ, where there is a spermatophore formed there can be no such function. Second, nor is it true in the sense that it is formed by a growing together of the two *vasa deferentia*. It is formed by an invagination from the outside, as was first shown by Palmen (*17*) from the anatomical standpoint and by Nusbaum (*16*) from the embryological. This invagination projects quite far beyond the point at which the two *vasa deferentia* join it (fig. 7). It extends dorsalward and forward, where it receives the openings of the hundreds and hundreds of tubules of the annexed glands (fig. 9). The lumen is very much flattened laterally and widened vertically towards the blind end. The more muscular tube leaves the sinus at the posterior dorsal angle just above the point of entrance of the *vasa*. This is well shown in figure 9. The openings of the *vasa* cannot be recognized in this figure, but the serial sections leave no doubt as to its location.

The hundreds of glandular tubules which empty into the upper end of the common duct vary greatly in length and diameter, apparently depending in part upon the room they find for development (figs. 6, 7 and 9). They take up all the available space, completely surrounding the seminal vesicles, extending far backward beside the rectum and the spermatophore pouch, or crowding forward and upward around the intestinal tract. Many of them are short while others are long. The whole group of tubules forms a large mass which takes up quite a space (fig. 6).

The "prostatic gland," first noticed by Berlese and later described by Fenard, I found "only after much difficulty," as the latter says. From my dissections I had concluded that the part so described was a part of the irregular pouch which molds the plate of the spermatophore. But a careful study of serial sections reveals the presence of a pair of oval glands or pockets attached on either side to the common duct. They have very short connecting tubes and they lie in the muscular and connective tissue surrounding that part of the common duct between the ganglion and the mold. The glands are not surrounded by "yellowish fat," as Fenard suggested; but they have "thin walls and are filled with a clear fluid." This fluid seems to harden into a clear yellowish chitin-like substance when treated with fixatives. In this it resembles the secretion from the annexed glands; but their secretion is darker and more granular. Judging from the behavior of the secretion and the position and connections of these glands I think they do not furnish a lubricant, but probably have something to do with the formation of the more flexible thread and the plate.

The common duct, after passing close to the floor of the abdomen, turns dorsalward and then empties into the cavity of the spermatophore mold (fig. 9). This apparatus was carefully studied by Lespes (*11*). Many of his observations are keen and to the point, but his description in some points is not very clear. Berlese (*4*) studied this structure too, but he could not get away from the idea that he was dealing with the ordinary structures, so he applies the name "penis," etc., to the parts and so makes his description misleading. Fenard (*6*) pays no attention to the hard structures and so he does not make out the relations and functions of parts in this region. Peytoureau (*19*) studied mostly only the morphological rela-

tions of the hard parts and so he does not explain the functions of the parts of this organ.

Lespes describes this apparatus "charged with the formation of the spermatophore" as follows:

"It is situated at the posterior part of the ejaculatory duct and may be considered as a part of the genital armature. In the field cricket this armature is formed, first, by a curved plate composed of many pieces extending to the right and left and united by a tough membrane; and second, by a very remarkable independent inferior part. The plate itself is composed of six solid pieces. Above is a kind of shield-like piece which is easily divided along the median line. Posteriorly it ends in three hooks, of which the middle one plays an important part in copulation. To the right and left are long slender rods upon which are inserted the fleshy pallets which support the vesicle of the spermatophore. Below this shield are two others, thin and curved, with an irregular contour. Finally, on the inferior face of the dorsal shield are two small, slender plates. During copulation the median hook only enters the vagina and serves to conduct the plate of the spermatophore. The independent piece is formed in front by a sort of short stylet which is applied to the inferior face of the plate of which I have just spoken. At the base this stylet enlarges, changes its nature and forms a white plate with cross striations. This plate is bent along its length, forming an irregular circle. It is swollen into a very thin vesicle situated under the genital armature and in front of the two pallets which support the ampulla of the spermatophore. This pocket is largely open in front and under the genital armature. The ejaculatory duct, after having passed around the lower part of the spermatophore pouch, ends near this opening.

"This white plate is the organ for the production of the spermatophore. On its convex surface is a transparent line in which is formed the tube which holds the thread of the spermatophore. The size of the plate is greater at the two ends. At the terminal part of the enlarged inferior portion ends the ejaculatory duct."

Lespes claims to have seen the spermatophore while it was forming. "It had a very thin membrane. When completely formed the vesicle was removed out to the place between the two fleshy pallets, and the plate and the thread remained in

the forming organ, that is, in the stylet of the armature, until given off to the female."

This description is somewhat indefinite because of the uncertain meaning of the phrase "genital armature." Besides, the application of the words "in front" and "behind" is not certain. I do not believe that the differences between Lespes's description and my observations can be accounted for by supposing such differences exist in the different species studied. Both of us used *Gryllus domesticus* some, and as shown below we found only small minor differences between the house cricket and our own species of field crickets.

Before discussing the formation of this peculiar spermatophore farther let me state as clearly as possible the mechanical problem involved. There is a mold made up of a system of bracing rods of chitinous material and a thin fibro-muscular membrane. Into this mold leads a single tube, which has to bring the sperm and the secreted fluid for the covering. The ampullar part of the finished spermatophore has apparently a double wall, and so there may possibly be two kinds of secretions, although a careful study of the gland shown in figure 10 makes me doubt it. The question is, then: How are the sperm kept separate, and especially how are they *held* in the center while the soft liquid is poured around them and hardens? If there is a second layer in the wall the incomplete ampulla would have to be held in the center while the second inflow and hardening occurs. To place a semifluid substance within another fluid substance and hold the former at the center while the latter hardens would be a difficult feat for any mechanic. I do not see how the apparatus provided is sufficient to accomplish the result. Yet I have seen so many well-formed spermatophores that there can be no doubt of the end product.

The way to solve the problem readily suggests itself. One needs to get a lot of specimens showing the various stages in the formation of the vesicle. Such a series of stages I have been hoping to get, but have thus far not succeeded. In all my many dissections I have never found a partially formed vesicle. It is hardly feasible to follow the process in a living specimen, as the attempts to make observations would interfere with the normal formation.

Although I am not able to give a description of the exact method of formation, I shall nevertheless make some sugges-

tions. Lespes says that the ampulla is formed and then moved out to its position between the two pallets. I think that this cannot be correct, as it would mean that the plate and thread would have to be joined onto the ampulla. In all the specimens I have seen the inside cavity and the walls are just as smooth as they can be. I cannot imagine that if the apparatus is formed in two parts they could be joined together so exactly and smoothly. I would rather believe that the structure is formed as a whole *in situ*. The thing that gave the idea that it moved back is the fact that when the wall has partly hardened the pallets retract a little, exposing the ampulla.

When there is no spermatophore in a male cricket the hooks are drawn far down, the pallets are much contracted and folded, and a part of the loose tissue on the floor of the cavity is rolled up and fits into the mold as a sort of plug. The pallets and the plug have deeply grooved and ridged surfaces which line the small lumen within.

Things occur about as follows when a spermatophore is formed: The inner lumen becomes a little larger and assumes the shape of the cavity of the vesicle. Then the sperm pass down, filling it up. It is possible that the lining cells secrete a small amount of substance to form a thin membrane, and Lespes may have found an example in this stage. If a membrane is secreted it cannot be discerned later. Now some secretion comes down the common duct. This flows in and fills up the grooves. The ridges withdraw, forming new grooves to be filled up. The process continues till enough is laid down to form the inner layer of the wall. Then the flow ceases for a while, and the secretion hardens somewhat. After a longer or shorter time a second inflow of secretion occurs, and it takes the place of the withdrawn ridges till the surface of the lining membrane becomes smooth, thus forming the outer wall of the ampulla. Then the whole hardens into the completed spermatophore. I think the whole takes place in a short time relatively. There may be movements accompanying the process, although I have not observed them.

Since there is but one duct, the only other assumption which could be made is that the secretion and the sperm come down all together instead of in succession. If this be correct, then the long sperm would have to wiggle their way to the center. This is hardly possible. Besides, it would be difficult to explain the second layer in the wall of the ampulla by this hypothesis.

Another mechanical problem appears in the study of the spermatophore, namely, What causes the sperm fluid to flow out of the ampulla? Are they forced by contraction of the walls, or is there some substance that swells and forces them out? Does air penetrate the wall in some way and thus prevent a vacuum?

I do not believe that there is any contraction; at least not much. The walls do not collapse. Farther than this I could find nothing that would throw any light on the problem.

Differences Found in the Domestic Cricket.

Lespes describes the spermatophore and the spermatophore-forming organ of this species, but says that he has not seen the act of copulation. I can readily believe the latter statement, as the insects are much more shy and will not mate readily when watched. Nevertheless I witnessed the process several times. The behavior during courting and the movements during the transfer of the spermatophore are very similar to those of the field crickets. The differences are of no consequence.

The spermatophore is lighter in color, as Lespes says. But this is in accord with the general lack of color in this species. It is a little shorter and stouter, as the Frenchman indicated. The plate is also narrower and more bent. But the cavity does not extend back into the papilla, as I have already explained about our field crickets.

There is one point to which I should like to call attention. Lespes does not speak of it, yet shows a difference in the drawings. In the house cricket the thread is a direct continuation of the canal. This is correct for this species, and is precisely what I find in our field cricket. I have not seen the spermatophore in *G. campestris;* but judging from our domestic and field crickets, and the conditions I find in *Nemobius*, I do not believe that Lespes is correct when he indicates a break between the thread and the plate, as he shows in his drawings, figure 2. The canal could not be continuous if his drawing is correct. But Lespes thought that the thread was the mass of sperm, and so not thinking of the thread as a hollow conducting tube he might have a break in it.

The mold differs from that of our field cricket about as it differs from *Gryllus campestris,* judging from Lespes's description. The hooks on the superior plate are rudimentary or

absent, while the stylet is well developed and projects far backward. The cavity is smaller, making it necessary that the plate of the spermatophore be bent into a smaller curve. There are other minor differences in size and relations. Whether these differences are great enough to prevent intercrossing of species is not positively settled. I tried some experiments in cross-breeding, in which I was unable to get any cross matings; but the tests were not extensive enough to be very conclusive.

IN NEMOBIUS.

This genus resembles rather closely the form which Lespes describes under the name *Gryllus Sylvestris*. It is much smaller than our *Gryllus* and, like the European form, it likes the woods or shady places; in the grass under the trees of a park I have found the most specimens. In the months of August and September they are very numerous.

In its courting it is, like the domestic cricket, much more shy than the larger form, and it is rather tedious to watch till one catches a pair copulating. In the main the whole series of processes is quite similar to that in *Gryllus*. In the courting the male is more active while the female less readily yields to the courting. What Lespes (*12*) says of his forms holds true for our two genera: "Except some details of form and size all is similar. The spermatophore is smaller and more fragile but is similarly composed. The genital armature presents the same pieces, but they differ much in form." Lespes again in this species figures and describes the thread as continuous with the canal of the plate. This strengthens my belief that there is some mistake in the description of the spermatophore of *Gryllus campestris*.

I have succeeded in getting a good photograph (fig. 4), that shows the structure of the spermatophore of *Nemobius fasciatus*, our most common species, very well. The ampulla is almost a perfect sphere. Its wall is thick and its central cavity rather small and nearly spherical. As in *Gryllus sylvestris*, the plate is small and far from the ampulla, but the thread and plate are much more curved in our species (fig. 4). There is a fine, hollow, tube-like opening leading from the central cavity to the tip of the thread. There can be no doubt that the sperm fluid flows out through it.

IN GRYLLOTALPA.

Fenard (*6*) cites the fact that the Locustidæ and the Gryllidæ produce spermatophores and that those two families have the large mass of annexed glands. Continuing, he says: "Then wherever we find the glandular tubes similar to those in the above-mentioned groups we have a right to conclude, until there is proof to the contrary, that they secrete a substance destined for the formation of spermatophores more or less complex." He suggests that in *Gryllotalpa*, whose copulation has never been seen, fertilization occurs by means of a spermatophore, because they have the annexed glands similar to those of *Gryllus*.

In the abstract (*2*) I made the statement that in the mole crickets the sperm are transferred by means of a spermatophore. In order to observe copulation I kept four mole crickets, two pairs, for several weeks each in a separate aquarium partly filled with wet sand, grass roots and slices of potatoes. For five nights I placed them by pairs into battery jars which contained just enough sand to allow the animals to make a burrow around the edge. Thus I could watch them continuously. After some twenty hours I finally observed copulation. As a result of these vigils I am able to give the facts concerning chirping and the protective gland published elsewhere (*3*), as well as the following concerning copulation.

The courting is somewhat similar to that in *Gryllus*. The male calls the female with loud, long chirps. As she approaches the chirps become short and much softer. He then frequently turns his abdomen towards her. As the pair get ready to copulate the position assumed is quite different from that of any other animals of which I know. They turn posterior end to posterior end, and ventral side to ventral side, so that the cloacal openings are just opposite each other. The female stands erect with her abdomen slightly raised, while the male lies on his back. The abdomens are tightly held together by hooks, described with great detail by Peytoureau (*19*). The sperm were carried to the female by a spermatophore. The time it takes for the transfer is not over a minute; but the pair kept their relative position, the abdomens simply touching each other, for more than ten minutes. After disturbance the male followed the female and again assumed this

relative position, but no further transfer of a spermatophore occurred.

Right after the first separation of the couple the female began to chew at a part of the sperm vesicle, and only desisted when disturbed by the movements of the male. She was also perfectly quiet as soon as her abdomen was touched as in the position of copulation. One observation is not enough to establish the purpose of an act; yet, judging from the behavior of the individuals of this pair, especially from the anxiety of the male to touch the female with his abdomen, one could easily conclude that the long lying in the position of copulation was to prevent the female from chewing at the spermatophore too soon and thus preventing the proper injection of the sperm. After the pair had remained in the above-described position for ten minutes or more the female left the male and manifested no further desire to chew the spermatophore. She carried it for about a half an hour and then dropped it.

As the vesicle was being transferred, or just after it had been put in place, there was an outflow of some transparent fluid on either side of the vesicle. This soon hardened. It is this part of the apparatus that the female was chewing. The spermatophore was found to consist of an oval ampulla which contained the sperm in the cavity at the center. At one end of the ampulla there is a projection by which the apparatus is held in the vagina, and through which the sperm are carried into the spermatheca. On either side of this projection is an irregularly shaped mass formed by the above-mentioned outflowing fluid during the transfer. The two sides are unlike, as part of one side was pulled and eaten away by the female, and the other side was pressed out of shape by some falling sand before it had time to harden. Having but this one imperfect specimen of the spermatophore of these crickets I cannot give as accurate a description of its detail as I should like. Suffice it to say that it has the essential parts—a hollow ampulla to contain the sperm and a projecting part to fasten it to the female and to carry in the sperm. The structure of the latter is obscured by the irregular mass.

The outflow of this fluid recalls an observation which I made repeatedly in the Chicago greenhouses. In the copulation of a locustid the same phenomenon occurs, but in a more marked way. The species, an exotic one introduced from Japan, is

very abundant in the greenhouses. The male has no chirping organs and so the courting is all done by means of the long antennæ. The female mounts on the back of the male, when he hooks an almost spherical ampulla full of sperm into her vagina. During the latter act a viscid fluid flows out on either side and forms two somewhat irregular roundish masses larger than the original ampulla, which now lies between the two. Sometimes the female began immediately after copulation to eat this substance, doing it more readily if the couple was disturbed.

As to a use or meaning for this outflow of fluid and its subsequent hardening it is difficult to suggest a satisfactory one. Of its regular occurrence there can be no doubt, as I observed it many times in *Diastremmena* and once in *Gryllotalpa*. It may function as an additional fastener to hold the apparatus in the vagina. Yet this seems hardly necessary, as the spermatophore apparently remains in place before it is hardened. It may have something to do with the emptying of the vesicle, contracting around the ampulla, thus forcing out the sperm. Or it may be concerned with the removal of the spermatophore from the vagina, acting as a bait for the female to remove it.

SUMMARY.

1. The reproductive apparatus of *Gryllus* is not of the simplest type, as was reported by the earlier investigators and as is still suggested by our textbooks. These organs are rather of the most complex kind found among the insects. They were studied and described with a good deal of detail, and the correct method of the transfer of the spermatozoa was indicated by Lespes in 1855; but the work was discredited and neglected.

2. The male carries the sperm to the female in a special structure, the spermatophore, formed by the secretion of the glands annexed to the common duct.

3. The essentials of the spermatophore, as shown by the study of several genera of Gryllidæ, are a hollow vesicle to act as a retainer, and a hollow thread-like tube which carries the sperm into the spermatheca of the female. To the tube are added some enlargements which serve to hold the structure in the vagina.

4. The so-called genital armature of the male crickets consists of a mold for forming the spermatophore and an apparatus to transfer the same to the female.

5. The differences between the field and domestic crickets is probably great enough to prevent intermating, yet this is not at all proven.

6. *Gryllus* has no gland which secretes a lubricant for the copulatory organs. The so-called "prostatic gland" has to do with the formation of the thread and plate of the spermatophore.

7. Mole crickets form a spermatophore. A transparent viscid fluid flows out during the transfer. The male and the female assume a very peculiar position relative to one another during copulation.

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CONTENTS:

AN EXAMINATION OF THE CHROMOSOMES OF ANASA TRISTIS:
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AN EXAMINATION OF THE CHROMOSOMES OF ANASA TRISTIS.

BY C. E. M'CLUNG AND EDITH PINNEY.

I. Introductory statement.

II. The chromosomes during the spermatogenesis of Anasa, an independent study: By the junior author.

III. A comparison of the results of studies upon the chromosomes of Anasa: By the senior author.

1. Methods.
2. What is the number of spermatogonial chromosomes, and of oögonial chromosomes?
3. What is the number of first spermatocyte chromosomes?
4. What is the behavior of the accessory chromosome and of the plasmasome in the first spermatocyte prophase?
5. What is the behavior of the accessory chromosome in the first spermatocyte mitosis?
6. What is the behavior of the chromosomes in interkinesis?
7. What is the behavior of the accessory chromosome in the second spermatocyte mitosis?
8. What is the final chromosome constitution of the spermatozoa?

I. INTRODUCTORY STATEMENT.

The extensive studies now in progress upon the chromosomes of numerous species of plants and animals have led to the formulation of several working hypotheses of considerable general importance. In order that these may be of value and serve as an aid to further progress, it is necessary that the phenomena from which they take their origin be extensively recognized and uniformly interpreted. Any conception of the relations existing between germ-cell organization, as exhibited by the chromosomes, and the structural characters of the body is now unfortunately delayed by certain disagreements

upon the actuality of the phenomena upon which such interpretations are based.

Fundamentally, these disagreements concern more or less intimately that view of chromosome organization which is called the "theory of chromosome individuality." Modern cytologists are either supporters or opponents of this theory, and its adequacy or inadequacy will be determined by the weight of evidence now accumulating. It is, of course, impossible to conceive that it will stand unmodified, for it is but the expression of our present limited knowledge; but it must now be determined whether these structures of the cell have persistent individualities or whether they are merely incidental and inconstant expressions of more fundamental phenomena. Observed facts must support one or the other of these alternatives, although in doing so they may readily enough modify the established order.

A considerable body of evidence has accumulated within recent years to support the theory of chromosome individuality and to associate the development of sexual characters with particular chromosomes. To this has been added the support of experimental work on sex determination and the parallelism between the segregation of Mendelian characters and the behavior of the chromosomes in the maturation divisions of the germ cells. Much of this cytological work has been done upon the insects, particularly in the orders Orthoptera and Hemiptera, and, in the large, there is a strong consensus of opinion. More recently confirmatory evidence has been furnished from studies upon nematodes, including Ascaris, by Boveri, upon echinoderms by Baltzer, and upon birds and man by Guyer. Here and there, however, there are workers who question the fundamental facts and deny the correctness of the theories founded upon them.

It is necessary, in order to proceed further with our interpretations, that we reach an agreement upon the observable facts in our science, and no honest question should remain without answer.

At present one of the most serious diversities of opinion exists regarding the character and the behavior of the accessory chromosome in the bug *Anasa tristis*. Because of the extensive and painstaking studies of hemipteran germ cells by Wilson, the contradictions and inaccuracies in the studies of

Paulmier and of Montgomery seemed to be cleared up and the phenomena in this order brought into agreement with those of the other insects. To this was added the confirmatory work of Stevens upon several orders of insects, the study of Lefevre and McGill on *Anasa*, and more recently that of Morgan on aphids and phylloxerans. Directly opposed to all this are the observations of Foot and Strobell upon *Anasa tristis*, the form studied in detail by Paulmier, Montgomery and Wilson. Their contention, in brief, is that the number of spermatogonial chromosomes is even instead of odd, that there is no dimorphism of the spermatozoa due to the presence in one-half their number of the accessory chromosome, and that there is no evidence to show that the theory of chromosome individuality receives any support from observed morphological continuity of any of the chromosomes. Aside from these major questions there are others, such as the history and fate of the plasmasome, upon which these authors are in disagreement with other investigators.

The issues here defined are so clear-cut and definite and their settlement of so much importance that the senior author of the present paper was led to offer his services for a reëxamination of the whole question. This offer met a hearty response from Professor Wilson, who sent not only live material, but his entire series of mounted slides, including those used by Paulmier. Professor Lefevre has been kind enough, also, to permit the use of his slides. Miss Strobell, writing for Miss Foot, expressed a lively interest in the proposed settlement of this problem, but was unable to send the preparations used in their studies, because these had all been destroyed on account of limited storage room. It is to be regretted that this material is not available for comparison, since it is upon it that the only divergent observations have been made; but since specimens from the same locality, prepared by all methods, including the special ones employed by the Misses Foot and Strobell, are at hand, there can be no reasonable doubt that it is representative.

To reduce the possibility of the influence of preconception to the lowest possible degree, the junior author has worked through the entire problem without knowledge of the work done by others, and without promptings from the senior author except such as were given by a series of questions for

which answers were desired. Independently, the senior author went over the same ground, first upon material prepared in this laboratory, and later upon the slides of Paulmier, Wilson and Lefevre. Whenever possible, photomicrographs were made, and representations of them accompany the paper. The two authors reached concordant results throughout, and their common experience is embodied in what follows.

Since the matters of dispute are purely of facts and interpretations, it will be necessary to take a definite position on each of the points involved, but so far as possible the material evidence for the decisions will be presented fully. It is hoped that this may be complete enough so that others interested may be able to form their own opinions directly from the appearances themselves. There will be presented first the personal work of the junior author, giving her independent results, and this will be followed by a general discussion of the problem by the senior author.

II. THE CHROMOSOMES DURING THE SPERMATOGENESIS OF ANASA TRISTIS.

BY EDITH PINNEY.

Preparatory to an attempted settlement of various disputed questions in the development of the germ cells of *Anasa tristis* an independent reëxamination of the entire process was undertaken. In order to avoid unconscious bias of opinion the previous reports on the spermatogenesis of this species were not read. Without referring, therefore, to the accounts of other observers for comparison or correlation it is purposed to record the results of these observations.

Material.—Preparation and general description.

Material was taken from specimens of *Anasa* collected in Lawrence, Kan., and in Woods Hole, Mass. The latter was obtained through the courtesy of Dr. E. B. Wilson, of Columbia University. All material was fixed in Flemming's fluid, the period of fixation varying from one-half to two hours. The longer fixation was found to give the better results. Paraffin sections were cut five micra in thickness and stained by Heidenhain's iron-hæmatoxylin, Flemming's tricolor and Auerbach's methods. Slides prepared by the author from nineteen individuals were studied. Most of the drawings were made at a magnification of 3625 diameters. This is reduced one-half in reproduction.

The testes of *Anasa tristis* are paired organs in the form of two small fig-shaped bodies which lie on either side of the median line in the cephalo-ventral part of the abdominal cavity. They are composed of a number of long, slender follicles lying parallel to each other and extending the entire length of the testis. The follicles themselves taper slightly from the broader base toward the sperm-duct. The follicular organization into cysts of germ cells of varying stages of maturation is similar to that in the Orthoptera, and the same method which was used to determine the sequence of the observed changes in the Orthopteran species is applicable here. Practically all of the cells of a cyst are in the same phase, although exceptions to this regularity are frequent in the older cysts, particularly those of the first and second spermatocyte generations. These variations are, however, to be expected, and may reasonably be accounted for if one considers the unavoidable differences which must occur in the rate of metabolism in cells situated differently in the same cyst.

The longitudinal section of a follicle presents some noticeable features of a structural nature caused by characteristic differences in the cells of various regions. The spermatogonial cells occupy the distal portion of the follicle, the extent of the spermatogonial area being determined by the age of the individual. These cells are small, and in the older cysts the nucleus is accompanied by little cytoplasm. Hence the peculiar staining quality of the nuclear material causes this region to appear more intensely stained than the proximal portion of the follicle. The cells, too, are crowded closely together. In contrast to this is the lightly stained spermatocyte region, due to the fact that here the cells contain a greater amount of cytoplasm in proportion to the amount of nuclear material. The cells have increased so greatly in size in the later generations that the cysts are larger. Usually a characteristic barrier exists between the two main regions of divisions. This is formed by cysts of cells undergoing the process which has been designated as synizesis, a detailed description of which will come later. In almost every instance, too, the line of separation is emphasized by the presence of many cysts of degenerating cells with their spherical masses of chromatin.

OBSERVATIONS ON THE SPERMATOGONIA.

From a study of polar views of the equatorial plate the number of spermatogonial chromosomes was determined to be twenty-one, and in no case was there observed a departure from this characteristic number. The chromosomes in young cells are larger than those in older cells and do not exhibit the tendency to coalesce so readily. Consequently cells for studying the number, form and behavior of the chromosomes were comparatively few, although enough were found to leave no doubt in the observer's mind as to the correctness of these observations and their interpretation. Figures 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, show polar views of the equatorial plate from spermatogonial cells. Certain elements of the complex exhibit constant and striking characteristics in size relationships. The largest three chromosomes in each group are easily identified, as are also the smallest two. The remaining members of the group more nearly approximate each other in size, so no attempt was made to homologize these in the several cells.

The form of the chromosomes varies from spherical and ellipsoidal to kidney-shaped with variations in size and position. The smallest two elements show the most striking differences in these respects from the other members of the group. There seems to be no fixed arrangement of the individual elements, except that there is an evident pairing of twin chromosomes. Sutton reported the presence of similar pairs in *Brachystola magna** and his observations have been verified by other workers in this laboratory on other species of the Orthoptera.† One element of such a pair is considered to be of maternal origin and the other of paternal origin. The tendency for equal elements to get together is very marked even in young cells, and makes conspicuous the presence of an unpaired element, one of the largest three chromosomes. Should its mate exist in the cell it could not possibly be overlooked when even the smallest elements are so prominent. Owing to uniformity in size, precisely which of the three is the unpaired element may be decided upon only when two of them are unmistakably paired. The smallest two elements show this tendency but rarely, their behavior at this stage being consistent with subsequent irregularities.

* "Spermatogonial divisions of *Brachystola magna*." Kansas University Quarterly, vol. 9, No. 2, 1900.

† The Chromosome complex of *Syrbula admirabilis*. W. R. B. Robertson. Kansas University Science Bulletin, vol. IV, No. 13, 1908.

All of the chromosomes lie with their long axis in the plane of the equatorial plate, and from a study of lateral views of this stage it is evident that the plane of the split in the chromosomes coincides with the same plane. Ideal conditions for equal division of chromatin are therefore present. Division is simultaneous throughout the group. The separated halves move toward opposite poles, maintaining their relative positions until the pole is nearly reached. Thus the shape of the spindle during anaphase is altered to accommodate the varying conditions. See figures 12, 13 and 14. There is no evidence as to the method of spindle-fiber attachment, and it is doubtful whether the matter can be decided in this material. Figure 15 is a drawing of a section through an entire cyst. Most of the cells are in metaphase. A few are in anaphase. The polarity exhibited in this section is typical of all cells of this generation.

In lateral views of anaphases in young cells the chromosomes are distinct. In the older, more crowded cysts the tendency of the individual elements to coalesce produces the appearance of a solid band of chromatin in the equatorial plate. Later stages of the same show two separate bands with spindle fibers between. The plate arrangement is lost when the pole is reached. Figure 17 shows a polar view of an early telophase. The chromosomes have not yet lost their identity, although they have apparently begun to disintegrate. Between the telophase and the succeeding metaphase there is an increase in the amount of chromatin. The formation of a nuclear membrane and the further dissolution of the chromosomes follow. A typical telophase from a young cyst is shown in figure 18. The daughter nuclei are flattened, but assume a spherical outline as the diffusion of chromatin proceeds. Figures 19 and 20 show the culmination of this process.

The inauguration of the next mitotic cycle is marked by the appearance of an exceedingly long and much coiled spireme, whether continuous or not it is impossible to say. At any rate, after the thread has thickened and shortened considerably it is plainly seen to exist in segments which finally condense to form the homogeneous bodies of the chromosomes. Figures 21 to 28, inclusive, show the successive steps in this transformation. The shortening segments show various twists, bends and contortions. See figures 22, 23, 24 and 25. Not until very late in the prophase does the longitudinal split in the threads become

visible. (Figs. 26 and 28.) At this stage pairing of equal elements is very common throughout the spermatogonial generations. Note the marked pairs in figures 1, 2 and 4, plate LXV. It would seem from this that throughout the history of the spermatogonial cells there is a consistent provision for the final processes which mark the transition from spermatogonia to spermatocyte. This process is called synapsis. The cells of a mature spermatogonial cyst have not been counted, but judging from the number of cells in a cyst of developing spermatids, eight mitoses complete the activity of the germ cells as spermatogonia, that is, that after the last division there are 256 cells in a cyst. In such cysts the cells are poor in cytoplasm.

After the final division the typical telophase is replaced by synizesis. During this process the chromatin is contracted into a deeply staining granular mass whose position within the nucleus is either central or slightly eccentric, leaving the peripheral area clear. It is quite certain that the chromatin mass is composed of intimately associated granular threads, for occasionally ends protrude from the knot, although entire threads can not be traced. (Figs. 30, 33.) It is true that the chromatin enters synizesis in the form of individual threads, and the presynizetic stage is characterized by the same elements. It is reasonable to suppose that the threads continue as such during the period of synizesis. That some change is taking place within the knot is shown later, but there is no evidence to show that this change involves the disorganization of the chromatin threads and its reorganization into new elements. Nothing can be said in regard to the duration of synizesis. That an end to end conjugation of the paired elements of the spermatogonial nucleus occurs during this period seems established beyond a doubt.

At one side of the conjugating threads lies a definite chromatin body of homogeneous consistency. Occasionally this body shows an uneven outline suggesting a slight disintegration of the constituent chromatin. Its position is constant and it is invariably present. From a study of subsequent maturation processes it is shown to be the accessory chromosome (McClung, Orthoptera) and can be identified as the homologue of the unpaired element appearing in the spermatogonial metaphases. In studying the history of this odd member of the complex, drawings of it in that stage were made, as well as

in numerous subsequent stages, for size comparisons. Fig. 14, plate LXVI, shows several drawings from different individuals. The spermatogonial cells from which drawings of the accessory were made vary in age, and as there is undoubtedly a decrease in the chromatin content of these nuclei as the cells multiply we would naturally expect to find homologous chromosomes varying in size in the same individual. The position of the chromosomes with respect to the equatorial plane varies previous to division, that is to say, in the formation of the equatorial plate the chromosomes may lie obliquely to the plane of the equator, and this would cause apparent differences in the size of camera drawings. Conceding that these possible causes of size variation are sufficient to account for the slight variations in size of the accessory as shown in the drawings, we are forced to conclude that the size of this element in the spermatogonia is strikingly constant. A similar study of the homogeneous body observed in the nucleus during synizesis shows a like constancy in size. Although these two elements which appear at different times in the nucleus are so unlike in form we cannot but consider them as equal chromatin masses. Moreover, if synapsis is a conjugation of twin chromosomes, obviously the unpaired element of the earlier stages would take no part in this process. This evidence is sufficient to incline us to believe that the two masses are identical. Further evidence will be given to strengthen this conclusion. An account of the presynizetic stages or growth period will be given in the observations on the first spermatocyte generation.

The First Spermatocyte.

The earliest condition of the spermatocyte cell is the result of the disentanglement of the chromatin knot formed during synizesis. Even before the chromatin has spread to the nuclear membrane, and while the peripheral area is comparatively free from it, it is easy to determine that the chromatin exists in the form of granular threads or rods. See figures 1, 2, 3 and 4, plate LXVI. This diffusion of the chromatin threads makes possible the detection of a second body similar in size and staining qualities to the chromatin body described as present during synizesis. This body is not present before synizesis, is not apparent during the synizetic period, and is present afterward in the interior of the nucleus. The natural conclusion then is that this is a product of synizesis. Its staining qual-

ities indicate that it is composed of chromatin. The distinction between this and the accessory is only possible when the accessory lies close to the nuclear membrane, which is its usual position. In this respect it resembles the accessory chromosome of the first spermatocyte prophase of the Orthoptera.

The history of the three distinct nuclear components, active chromatin, accessory chromosome and plasmasome, will be followed separately up to the spermatocyte metaphase, beginning with the chromatin. The reorganization of the nuclear chromatin into typical spermatocyte chromosomes after diffusion is completed gives no hint of a reversal of the mitotic cycle. That is, the appearances which characterize chromosome reconstruction do not suggest a reversal of the changes which were observed to take place in the diffusing chromatin. The straight threads which typify the early prophase (figs. 1-4, plate LXVI) gradually elongate and finally are disposed into a fine reticulum at the intersections of which are very slight accumulations of chromatin. See figure 4, plate LXVI, and figure 4, plate LXVII. This might be considered as the climax of diffusion, for in this stage the chromatin is most evenly distributed throughout the nucleus. Subsequently there are more extensive accumulations of chromatin at certain points within the nucleus. These amorphous aggregations of granular chromatin gradually assume the form of loosely organized tetrads resembling a few of the types of tetrads found in the Orthoptera. Figure 16, plate LXVI, shows four types of tetrads taken from one cyst all of the cells of which are in the same stage of development; (*a*) shows the largest form. By analysis it is seen to be composed of four equal chromatids and represents the pair of the largest spermatogonial chromosomes conjugated. The disposition of maternal and paternal chromatids is indeterminable in this as well as in the forms shown by (*b*) and (*c*), which are different types of the cross. In each case two opposite arms of the cross are composed of portions of maternal and paternal threads lying parallel to each other. The ends of these arms are the synaptic ends of the chromatids, but whether the synaptic end of a chromatid represents the polar end, as is certainly the case in the Orthoptera,* it is impossible to determine. One of the other pair of opposite arms is composed of parallel maternal threads and the remaining arm consists of parallel paternal threads;

* Pinney, Edith, Organization of the Chromosomes in Phrynotettix magnus, Kansas University Science Bulletin, vol. IV, No. 14, 1908.

(*a*) shows a rod form in which the division at right angles to the long axis may or may not separate elements of opposite parental origin. It is impossible to ascertain whether these rod forms have passed through the cross stage, since some of the earliest recognizable tetrads have this form and keep it as they condense.

The manner in which these forms are evolved from two conjugated chromosomes of opposite sex, each split longitudinally, is similar to that described for the Orthoptera by McClung;* (*d*) is an unusual condition at this stage of the smallest spermatogonial chromosomes. Even in stages as late as those shown in figures 22 and 24, plate LXVI, the separate halves of this pair often lie on opposite sides of the nucleus. Just previous to the metaphase they approach end to end. The constriction between the two halves is never obliterated by a close union. Evidently synapsis has had no effect on the smallest two members of the spermatogonial complex, although they undoubtedly entered into the synaptic knot. Subsequent changes consist in the condensation of these filiform tetrads to form the homogeneous elements of the metaphase. As the chromosomes approximate the homogeneous condition they arrange themselves at the periphery of the nucleus. This tendency may account for the characteristic position of the accessory during synizesis, the growth period and the spermatocyte prophases. The same nuclear membrane which is formed previous to synizesis continues to function up to the time of a late spermatocyte prophase. At the latter stage there are present within the nucleus thirteen distinct bodies. Figures 10 and 11, plate LXVI, show two parts of the same nucleus appearing in adjacent sections. The thirteen bodies are drawn. These must represent the twenty-one spermatogonial chromosomes plus the plasmasome created during synizesis.

Before stating the homologies between these spermatocyte structures and those of the previous generation the history of the accessory will be followed, beginning with synapsis. In this connection the behavior of the new spermatocyte element, the plasmasome, will be reported. The time of appearance, the nature and source of these two bodies, have already been spoken of. It has also been mentioned that immediately after synizesis the two bodies are practically equal in size. In the succeeding

* McClung, C. E., '00, The Spermatocyte Divisions of the Acrididæ, Kansas University Science Bulletin, IX, 1, '02; The Spermatocyte Divisions of the Locustidæ, ibid., XI, 8.

diffusion stages the plasmasome increases in size and the distinction between it and the accessory becomes very marked. In these stages the accessory remains closely appressed to the nuclear wall while the plasmasome is located internally. See figures 3, 5 and 6, plate LXVI. This period during the diffusion of chromatin and the growth of the plasmasome can not be considered as belonging to the prophase of the first spermatocyte. The nucleus increases steadily in size, reaching its maximum when diffusion is complete, so we may consistently call this interval after synizesis the growth period. Its culmination marks the installation of important changes, one of which, the re-formation of the chromosomes, has already been described. The accessory meanwhile maintains its former position, size and staining qualities. During the prophase the plasmasome gradually diminishes in size, and finally disappears just before the metaphase. During this time, too, it does not stain so readily with chromatin stains. In the Heidenhain's iron-hæmatoxylin preparations the staining quality of the plasmasome varied with the amount of extraction in the iron-alum solution. Occasionally the plasmasome presents a vacuolated appearance. This may occur at any time during its history but is more characteristic of the beginning of its dissolution. Occasionally in the prophase there occur two small homogeneous bodies staining like the plasmasome. As the typical plasmasome is absent and the accessory present these are considered as fragments of the plasmasome. There is no regularity in their occurrence. The cysts in this condition are not frequent and the majority of their cells contain typical plasmasomes.

In later stages the plasmasome is identified by its shape, becoming spherical as it decreases in size. Figure 7, plate LXVI, shows a nucleus containing the plasmasome and the accessory. The difference in staining qualities is apparent. The accessory remains in its former position, its form to the observer depending on his point of view. Plate LXVII consists of a series of drawings showing the size relations of the accessory and the plasmasome at the time of synizesis, the growth period and the succeeding prophases. The drawing of nuclei at the top of the page show the condition of the active chromatin. They are numbered in the order of the changes which they present. For instance, figure 1 shows a nucleus during synizesis. The perpendicular column below figure 1, designated 1*a*, shows a

number of drawings of the accessory taken from cells in the same stage as figure 1. Figure 2 shows a nucleus of the stage immediately following synizesis. The perpendicular column, 2*a*, below figure 2 shows a number of drawings of the accessory taken from nuclei in the same stage as figure 2. The perpendicular column, 2*b*, beneath figure 2 shows a number of drawings of the plasmasome taken from cells in the same stage as that shown in figure 2. In the same way columns 3*a* and 3*b*, 4*a* and 4*b*, etc., are drawings of the accessory and plasmasome from nuclei such as are shown in figures 3, 4, etc., respectively. The horizontal columns *A*, *B*, *C* and *D* indicate the different individuals from which the drawings were made. The differences in size which are shown in these monoplane drawings depend upon the point of view of the observer. That the accessory is constant in size is easily determined by different focusings. From these drawings there is also found to be a regularity in the relation between the size of the plasmasome and the condition of the active chromatin of the nucleus. From the foregoing observations it is now clear that the thirteen nuclear structures present in the late spermatocyte prophase comprise one accessory, one diminished plasmasome, two small chromosomal elements of opposite parental origin, and nine ordinary tetrads.

Figures 1 to 10, inclusive, plate LXVIII, show typical polar views of the first spermatocyte metaphase. All of the groups shown are from different individuals, with the exception of figures 2, 3, 4, plate LXVIII, which were in the same section of the same cyst. As many as six of these views, all typical, have been observed in one section in one cyst. There are eleven chromosomes present, each of which, with the exception of the accessory, is composed of four chromatids. The plasmasome has disappeared, also the nuclear membrane. The chromosomes lie in a clear area surrounded by the cytoplasm. Nine of the complex, including the largest, form a rather compact ring, in the center of which appears the smallest member of the group. The relative positions of the chromosomes forming the ring vary. One chromosome lies outside of the ring. Figure 11, plate LXVIII, shows six of these outer chromosomes at this stage taken from the same individual from which figure 6 was made. So, also, figures 12, 13, 14 and 15 are drawings of the similarly located chromosome found in the individuals from which figures 7, 8, 9 and 10, respectively, were made. This

eccentric member shows remarkable constancy in size. Its size and its position suggest the accessory during synapsis. See figures 29, 30, 33, plate LXV. Figure 5, plate LXVIII, shows a polar view of an atypical metaphase. This condition was observed only twice in this material, both times occurring in different individuals. There appear to be twelve chromosomes present. In addition to the small chromosome within the ring, there are two large equal elements which are not large enough to correspond to any elements present in the typical metaphase. Only eight chromosomes form the ring. It must be that the missing one of the nine which usually form the ring is represented by the two small and unusual bodies which lie within the ring, one on either side of the small element, and that this is merely an accidental case in which synapsis did not occur. In connection with this supposition we recall the fact that synapsis did not occur in the small chromosome at the usual time. This similarity of action during the synaptic period may be significantly related to their similarity of position.

In a lateral view of a spermatocyte anaphase the same surface of the chromosomal elements is presented to the observer as is seen in the equatorial plate of the spermatogonial cells. By referring to figures 1 to 10, plate LXV, it will be seen that the chromatids have become slightly shorter and correspondingly thicker. Here again the smallest chromosome asserts its independence. In the spermatogonial cells these small chromosomes present spherical outlines. In the first spermatocyte generation, instead of shortening, as their fellows, they have elongated. Only in this element and in the accessory was the plane of division actually determined. Since the two halves of the smallest chromosome are never so closely united that we lose sight of their identity, it can be stated positively that division in this case is transverse and qualitative, causing the separation of maternal and paternal elements. Owing probably to the slight attraction exhibited between the halves of this chromosome division is effected while the other chromosomes are still intact. Lateral views of early anaphases invariably show this condition. Similar views of later stages show its separated halves preceding the larger diads to the poles. In the ordinary tetrads the formation of the crosses might be interpreted to have the same significance as is attributed to the like form in the Orthoptera, in which McClung

has shown conclusively that the first division plane is longitudinal. However, in this case there is no positive evidence to offer. The chromosomes enter the equatorial plate with their longitudinal axes parallel to the spindle fibers. Figures 16 and 17, plate LXVIII, show that the polar ends of the chromosomes converge toward the poles of the spindle. That both methods of division may be employed by different members of the group is shown by a study of the accessory at this stage. This element, which is composed of two chromatids, was last observed in the metaphase lying outside of the ring. The element (x) in figure 16, plate LXVIII, is undoubtedly the accessory chromosome. This drawing is not limited to one plane. The small chromosome is shown dividing in its usual manner. This element, it will be remembered, is located at the center of the ring and no element of the ring could lie so far from this center as the one marked (x). This, then, must lie on the outside of the circle. From the arrangement found in polar views of the metaphase one would expect in the lateral views to find sections which would show four chromosomes in the same plane. These would include the small central member, two chromosomes of the ring, one on either side, and, at one side, the accessory. Such a section is shown in figure 17, plate LXVIII. The small chromosome, it will be seen, occupies the axis of the spindle, which in this view appears asymmetrical, the asymmetry being due to the extra divergence of the fibers attached to the accessory.

In these lateral views of anaphases the structure of the accessory is easily determined. It is composed of two chromatids, which are shown in figures 19, 20 and 21, plate LXVIII. All of the other chromosomes contain four chromatids, although in some only two of the four appear in the same plane. The accessory is easily identified by its form in these stages, where it is shown to divide tardily, division not beginning until the ordinary chromosomes have entirely divided. In their journey to the poles the accessory chromatids lag behind the others. Figures 17 to 26, plate LXVIII, show this behavior at different stages. All of the chromosomes of the complex keep their relative positions until the pole is reached. Figures 1, 2, 3 and 9, plate LXIX, show polar views of the dividing groups with the inner and outer members in their characteristic positions. As soon as the pole is reached the

chromosomes crowd together and, on account of the lagging of the accessory, lateral views of this stage show the condition reproduced in figures 25 and 26, plate LXVIII; (x) is the accessory. It is easily identified in both daughter groups. Figure 24 shows the only case observed which might be interpreted as the failure of the accessory to divide. The spherical form of the structure (x) may indicate a degenerate form of the accessory or an unusually persistent plasmasome. The crowding together of the diads at the poles completes the cycle of changes occurring during the first spermatocyte generation. No telophase involving the disintegration of the chromosomes and the appearance of a new nuclear membrane occurs.

The Second Spermatocyte.

The second spermatocyte generation begins with the formation of an equatorial plate by the members of the new spermatocyte nucleus. These second spermatocyte chromosomes consist of ten diads and one monad or single chromatid, the accessory. In figures 1, 2, plate LXIX, of typical equatorial plates of this generation will be seen a tendency toward the same chromosome arrangement which prevailed during the preceding mitotic cycle. From the size relations shown in figure 4, plate LXIX, which is a group of accessory chromosomes from cells of the same stage and animal as figure 3, plate LXIX, respectively, we are justified in our conclusions as to the identity of this element. Figures 5, 6 and 7, plate LXIX, are polar views of beginning anaphases. The chromosomes are viewed here in cross-section. Figures 10, 11 and 12, plate LXIX, show lateral views of the beginning of this ultimate division. Figure 10 suggests what transpired between the stage shown in figures 1, 2 and 3 and that shown in figures 5, 6 and 7. The transition is extremely brief, for evidence of it is comparatively infrequent. The chromatids which, during the first spermatocyte division, lay parallel to each other have separated at one extremity and have swung around until they lie end to end, the separate ends pointing toward opposite poles. The chromatids maintain this position during a relatively long period of time, for this condition and the following telophase are most commonly noted in cysts of second spermatocytes. A typical spindle is formed and the fibers are attached at the separated ends of the chromatids. Separation of chromatids occurs simultaneously, the smallest member here acting in unison

with the others. This may be regarded as due to the fact that the same conditions are present in all of the chromosomes previous to division; that is, the degree of union between the chromatids is the same in each diad, while it will be remembered that this relation between the diads which composed the tetrads of the first spermatocyte varied.

When the chromosomes separate sufficiently to expose a clear zone of fibers in the region occupied by the equatorial plate we find the accessory chromatid still in its place, and it keeps this position until the remaining chromatids have almost reached the opposite poles. Figures 13 to 18, inclusive, plate LXIX, show the successive steps in this division. Well coalesced daughter groups of this division are observed at opposite ends of the spindle, while the accessory lingers half way between. The accessory finally approaches one of the groups and almost immediately the dividing cell wall is formed. This leaves the accessory near the newly formed cell wall, entirely apart from the group to which it evidently belongs. Figure 19, plate LXIX, is a group of such bodies drawn from cells in this stage. The size of this lagging body was thus found to be constant. The spindle fibers between the two groups persist until after the nuclear membranes of the daughter cells are formed. Before this occurs, however, the changes shown in figures 20 to 25, inclusive, plate LXIX, take place. This consists in the withdrawal of the accessory from its position near the dividing wall into the now shapeless chromatin mass of the new nucleus. In studying these processes it was very easy to obtain sections which showed the two daughter cells in the same plane. The connecting band of spindle fibers leaves no doubt as to their relation even after the new cell wall has been formed. The accessory occurs in only one of these cells. A further significant fact is that in every such case where both daughter cells can be identified beyond doubt one always shows the accessory at some stage of its characteristic activity, while in the other no corresponding body is to be found.

As soon as the membrane forms around the spermatid nucleus which contains the accessory this element becomes detached from the mass of which it forms a part and moves again to the nuclear wall. Its individuality again becomes prominent. Figures 26 to 31, plate LXIX, show this condition. Here also the same precautions in determining its identity were observed.

Care was taken to study both daughter groups, in one of which it invariably occurred while the other offered no evidence of the presence of a similar element. The constancy in size of the accessory and the relation of its size here to the size of the accessory as determined by figures 4 and 19, plate LXIX, help to establish its identity. This condition of the chromatin in the spermatid nucleus lasts for only a short time. The large chromatin mass soon begins to break up into smaller masses which eventually distribute themselves against the nuclear wall. In an early stage of this disintegration the accessory is still easily recognized, as it lies on one side of the nucleus apart from the rest of the chromatin. It still keeps the elongated form it displayed in the second spermatocyte anaphase.

A whole cyst of young spermatid nuclei was counted in order to determine in just what proportion of the spermatids of one cyst the accessory occurred. The importance of this observation is obvious, although it seems that the result could be predicted safely from the evidence obtained from previous observations. An account of the method used in counting may help to verify the results. Serial sections of an entire cyst were obtained. The cyst chosen for counting ran through twenty-four sections. The sections were five micra in thickness. The exact condition of the chromatin was found to vary in almost every cyst of this generation. In the cyst counted were found the stages shown in figures 28, 29 and 31, plate LXIX. From the conditions existing in such nuclei we would expect to be able to identify the accessory from its shape and its position with respect to the rest of the chromatin in the nucleus. Evidently the number of nuclei in such a cyst and the number of spermatids formed would be equal. All whole nuclei or almost whole nuclei and fragments containing the accessory were counted. It was impossible to avoid the error of counting one nucleus as two where a nucleus happened to be cut exactly in half; one half appearing in two adjacent sections. The number of nuclei containing the accessory was 484. The number of fragments of nuclei which contained the accessory was 40. Thus the entire number of spermatids in which the accessory occurred was 524. The number of nuclei counted which contained no accessory was 577. These, however, would include the nuclei from which small fragments containing the accessory had been severed.

That would make the number of nuclei with no accessory 537, which is slightly larger than the number with the accessory. It has been pointed out that the nuclei which were cut in two equal parts might be counted as two. This would add to the number of cells which did not contain an accessory. Considering this source of error the number of cells of each kind may practically be considered as equal. There can be no doubt as to the occurrence of two kinds of spermatids which develop into spermatozoa, one containing one more chromatid, the accessory, than the other; and from the evidence presented we feel justified in concluding that the two kinds of spermatozoa occur in equal numbers.

III. A COMPARISON OF THE RESULTS OF STUDIES UPON CHROMOSOMES OF ANASA.

BY C. E. M'CLUNG.

1. *Methods.*

The methods of an investigator are a very important factor in arriving at conclusions, and it is quite possible to secure diametrically opposite results upon the same material by varying the technical processes. It will, therefore, be necessary to consider the methods of preparation and study employed upon *Anasa*. Paulmier, Montgomery, Wilson, Lefevre, McGill and Pinney fixed their material with Flemming's fluid, corrosive-acetic mixtures, Bouin's fluid and various other cytological reagents. This material was then sectioned in paraffin, and stained, principally with the iron alum—hæmatoxylin stain of Heidenhain. The slides thus prepared by Paulmier, Wilson, Lefevre and Pinney are beautiful examples of cytological technic and leave little to be desired in delicacy and precision. A considerable number of the slides sent me by Professor Wilson and Professor Lefevre are prepared according to the methods of Foot and Strobell, so that I have been able to study the material under their conditions, although, unfortunately, their own preparations have not been accessible to me. Since the entire case of these investigators, as opposed to all their fellow workers, rests upon their own peculiar methods, it seems desirable to consider in detail the technic upon which they rely.

The usual methods of cytologists are dismissed with practically no consideration, and instead of fixing the material, it

is spread upon glass slips and allowed to dry. (Foot and Strobell, '07, p. 282.) In this condition it is stained with Bismark brown and mounted in balsam. Entire reliance is placed in this method, and little attempt is made to correlate the results thus obtained with the appearances presented by other systems of technic. That the position of these authors on this point may be clearly understood, I quote their statement of the case.

"Professor Wilson, in his recent paper in *Science,* February, '07, replying to our preliminary note, says that he thinks the contradiction in our results is probably due to the difference of method employed, we having placed our faith in smear preparations, while he has relied on sections. We are glad of an opportunity to emphasize this faith, believing that for demonstration of the structure and count of chromosomes our modified smear preparations are more reliable than sections; and it is for this reason we have abandoned the use of sections in studying chromosomes, except for comparative work and for studying the topographical relation of the cells. In cells fixed and sectioned nearly all the delicate details shown in the chromosomes of our smear preparations are completely lost, and it ought to be too obvious to mention that a method which presents clearly each individual chromosome in its integrity offers decided advantages when the question of accurate counting assumes the importance and develops the contradictions familiar in recent literature."

The authors state that they have used sections for comparison and topographic work, but none of their photographs are made from sections, and their entire argument, as published, is based upon material prepared according to their own method.

It is my judgment that this method, *used alone,* is entirely inadequate for accurate results, and in this particular case is responsible for the discrepancy between these investigators and Paulmier, Wilson and Montgomery. From the work of Miss Pinney it will be clear, I think, that in the prophases figured by Foot and Strobell there are two darkly staining bodies, the accessory chromosome and the plasmasome, instead of the one shown in their photomicrographs. Owing to the technic employed by them the plasmasome is practically destroyed, and instead of using other methods to determine the

nature of the nuclear body, they *assume* that it is a plasmasome. "As the presence of a plasmasome in the nucleus at these stages is the typical phenomenon familiar in all known forms (its absence being most exceptional), we feel justified in interpreting the structure we find in the resting nucleus as a true plasmasome, and not an odd persisting spermatogonial chromosome, *i. e.*, chromosome nucleolus." (Foot and Strobell, '07, p. 284.) Further, the smear method does not give precise and accurate pictures of the chromosomes. The variation in size, owing to the different thicknesses of the smear and amount of spreading, is very extensive, as may be seen by a comparison of the photomicrographs of Foot and Strobell. Compare, also, figures 21-26, plate LXX, which represent smears of cells in the same stage. Not only may the entire groups of chromosomes in similar cells vary as three or four to one, but the members of one cell may suffer unlike expansion or contraction to a similar extent, if the conditions of drying are variable, due to the thickness of the smear film. There is but one advantage of the smear method over sections, and that is that it presents all the elements of the cell in one plane, so that their entire outline is visible for studying and photographing. It is a method that should be used in connection with sections, and from the beginning of my work I have utilized it consistently and with great profit in this way. I therefore speak of it as a warm friend and advocate, but at the same time I realize its limitations and am convinced that it should not be used to the exclusion of all other methods.

Foot and Strobell have employed photography alone as a means of presenting illustrations of their material, and it is assumed by them that if a thing can be photographed it must necessarily be a true picture of normal conditions. This I consider to be a decided fallacy. A photograph is an interpretation by the observer, just as is a drawing. The personal factor is no more absent from one method of illustration than it is from the other. Photographs may present with greater fidelity the details of structure in an object, but the choice of the object and the nature of details are at the command of the photographer. It is possible, especially in smear preparations, to select cells that will illustrate almost any condition and to photograph them. The highly interpretative character of the photograph is illustrated admirably by the present con-

troversy over the chromosomes of *Anasa*. Foot and Strobell publish photographs that seem to show that the accessory chromosome divides in the second spermatocyte division. This is their interpretation of the behavior of this element, and they illustrate it by photography. Not a picture which they publish would indicate that there is ever a case where the accessory chromosome positively fails to divide at this time, and yet literally thousands of unquestionable cases of this occur in every good preparation. See the group of cells shown in figure 15, plate LXXI. By selecting a series of early anaphases, and a very few obscure and distorted individual cells, they are able to secure pictures which appear to bear out their contention. In speaking thus of the methods of Misses Foot and Strobell, I wish it clearly to be understood that I am not reflecting upon their motives. It is my desire only to show that photographs are interpretations of observed phenomena and have no claim to infallibility. Again, as in the case of the smear method, I would state that I speak as a friend of the method and not as one who deprecates it. I believe that scientific papers, particularly cytological, should, whenever possible, be illustrated by photographs, and in my own publications I have followed this plan so far as the circumstances would permit.

2. *What is the number of spermatogonial chromosomes and of oögonial chromosomes?*

Confessedly, the accurate estimation of the numbers of chromosomes in these generations of cells is a difficult matter, and if it were the only means of determining the chromosomal differences of the sexes there might be occasion for doubt with regard to theories founded upon such enumerations alone. Fortunately, it is only one of several criteria of sexual differentiation in the germ cells, and so is not of commanding importance. Accurate counts of the chromosomes, however, are entirely possible with care, and concordant results are obtainable by independent observers. In the case of *Anasa* this is quite possible, and both Miss Pinney and myself have found the number twenty-one uniformly present in the spermatogonia. Not a single instance of twenty-two chromosomes was found in any spermatogonium, and we must therefore conclude with Wilson that thirty-one is the normal spermatogonial

number. In plate LXX, figures 1-3, may be seen spermatogonial complexes showing this number clearly.

It is claimed by Foot and Strobell that the number is twenty-two, and they publish four photographs in support of this view. Only one of these represents a stage where the chromosomes are compact and homogeneous, and this shows twenty-one chromosomes, although in the explanation of the figure the authors state that one of the apparent chromosomes is really two joined at right angles. Since there is no case in the figure where one chromosome is bent at almost right angles, the explanation is not very convincing. The remaining three are of earlier stages, in which the chromosomes have a loose structure that might readily be disturbed in the process of smearing, thus separating one of the larger chromosomes. In two of the photographs such an interpretation would seem to be entirely justified. Photo 49 is the only one in which there would seem to be any certainty with regard to the number twenty-two. Here it appears as if conditions were normal, and it might be recorded as an instance of twenty-two chromosomes in the spermatogonia.

The conditions regarding the spermatogonial number may be summarized thus: Paulmier, Montgomery at the time agreeing with him, reported twenty-two spermatogonial chromosomes. Later, Wilson, working upon Paulmier's original preparations in part, finds twenty-one spermatogonial chromosomes, and Montgomery, restudying his own material, agrees with this enumeration. Lefevre and McGill report twenty-one spermatogonial chromosomes from their own preparations. Foot and Strobell, working upon smear preparations, consider twenty-two to be the normal spermatogonial number. Miss Pinney, upon examining material from Kansas, Massachusetts and Pennsylvania, and working without a knowledge of others' results, finds twenty-one to be the spermatogonial number. Finally, from a study of the original material of Paulmier, Wilson, Lefevre and McGill, and Pinney, I myself find in all clear cases, where there is no doubt of the presence of all the chromosomes, that the number is twenty-one. Foot and Strobell object to the testimony of Montgomery, and of Lefevre and McGill, on the ground that they reported at one time an even number of spermatogonial chromosomes and at another an odd number. It must of course be admitted that this weakens their

testimony, for it is an evidence either of careless work or of the influence of preconceptions. I can recall with what difficulty I persuaded myself, against the current conceptions of chromosome numbers, that the spermatogonial number of chromosomes is odd in the Orthoptera, and I can easily understand the temptation, in an early stage of an investigation, to seek concordance with accepted opinions. The investigators who reported even numbers for their material did so when all the evidence from other forms seemed to demonstrate the universality of this phenomenon. In a sense their testimony is more valuable after a restudy of their material, because it indicates the desire to arrive at facts regardless of consequences. It is a very unusual man, or a very stubborn one, who finds no occasion to change his opinions.

This is the present status of the question concerning the spermatogonial number of chromosomes in *Anasa*. If it is impossible for the interested cytologist to come to a conclusion regarding the facts of the case from the studies so far made, he is quite at liberty to undertake an investigation for himself and I have no doubt but that all the material that has been available for my investigation will be placed at his disposal.

There appears to be no dispute regarding the oögonial number, although the counts in these cells have been less numerous than in those of the male. So far as the opportunity has offered I have gone over the female complex of chromosomes, and I have no reason to doubt that the number is twenty-two, as determined by Wilson.

3. *What is the number of first spermatocyte chromosomes?*

Regarding the number of first spermatocyte chromosomes, there seems to be no difference of opinion, since every observer has recorded eleven as typical for this generation. The clearness with which the chromosomes of the first maturation mitosis appear in the equatorial plate almost precludes the possibility of error. Here also may be found a close adherence to a type of arrangement which presents the small chromosome in the center, surrounded by a more or less regular ring of nine chromosomes upon the outside of which is placed the accessory chromosome. This is not an invariable arrangement, for it is a culmination of the movements of the chromosomes in the prophase where the elements bear somewhat similar relations to each other, but it appears in a large proportion of the cells.

The position of the accessory chromosome upon the outside of the group has led Foot and Strobell to coin another new name for it, and in their terminology it is the "eccentric chromosome."

4. *What is the behavior of the accessory chromosome and of the plasmasome in the first spermatocyte prophase?*

While there is no dispute regarding the number of chromosomes in the first spermatocyte, there is serious divergence of opinion with reference to the structure of the accessory chromosome. Upon its nature depends the number of spermatogonial chromosomes and the character of the four spermatids derived from each first spermatocyte, so its determination is most important. If it be a tetrad then the spermatogonial number must be even and the spermatids all alike in the possession of eleven chromatids; but if, on the contrary, it be a diad the spermatogonial number of chromosomes is necessarily odd and the spermatids of two types, one of which possesses eleven chromosomes and the other ten.

With the exception of Foot and Strobell all observers are agreed that there are but two chromatids in the accessory chromosome, but these observers claim that it possesses four as do the other chromosomes. As proof for this contention, they publish a series of chromosome groups from the late prophase in which the various elements are clearly shown. The identification of the accessory chromosome is correctly made in each case, I believe, but it is entirely clear to my mind that there is nothing in the appearance of these photographs to justify the interpretation of the accessory chromosome as a tetrad. There is in each case a characteristic difference between the tetrads and the accessory chromosome, for in the former there always appears a diamond-shaped opening, the angles of which point to the two lines of cleavage, while in the case of the accessory chromosome this is lacking. Every accessory chromosome, on the contrary, shows a clear, straight line of division along its entire length. In but a single instance is there an exception, and that is in their figure 4, plate II, where the plane of longitudinal cleavage is interrupted by transverse markings. A careful examination of this chromosome will demonstrate, however, that there is not only *one* of these apparent cross divisions, but *two* of them. I am convinced that the excellent photomicrographs of Foot and Stro-

bell of this stage are sufficiently clear in their evidence of the nature of the accessory chromosome, and I have not included any number of these stages in the photomicrographs accompanying this paper. Moreover, in none of the material that I have examined is there any indication whatever of a tetrad structure in the accessory chromosome, and I am thoroughly convinced that it is a univalent chromosome.

If the earlier prophase of the first spermatocyte be examined, the chief error of Foot and Strobell becomes evident. It is claimed by these investigators that the accessory chromosome behaves during the prophase as do the other chromosomes and that there is but a single nucleolus-like body present —a plasmasome. The work of Miss Pinney showing the transition in form and size of the accessory chromosome and of the plasmasome, both of which appear simultaneously in the nucleus, makes it entirely clear that Foot and Strobell were mistaken on this point. As I have elsewhere pointed out, the technic of these investigators is responsible for their failure to find the plasmasome, for it is this structure, and not the accessry chromosome, that is missing from the smear preparations.

These investigators have pointed out the large difference between the appearance of the accessory chromosome in drawings made by Wilson and the photographs illustrating their own paper. Such variations in the form of this element will receive explanation in part from the series of drawings made by Miss Pinney to illustrate the transition in form of the prophase elements. Both the stage of development and the method of preparation influence the form of this accessory chromosome. As a rule, sections show this element as a spheroidal, apparently homogeneous body during most of the prophase, but occasionally, just succeeding synizesis, it appears as a short, thick thread, with a tendency to be bent at the middle. This is the nearest approach to a spireme condition that it attains, and in this corresponds to similar conditions which I have described for certain Locustids. So far as my experience goes it would seem to be the rule that the accessory chromosome, to a certain degree, undergoes a granular diffusion of the chromatin similar to that of the other chromosomes, but that it is less extensive and is frequently marked by the close approximation of divisions of the thread.

It will be observed from plate LXX, figures 4-6 and 11, that

the accessory chromosome in this spireme condition is accompanied by a large distinct plasmasome which lies toward the center of the nucleus. Such a structure is absent from the photographs presented by Foot and Strobell when the accessory chromosome (their plasmasome) is elongated. As will be noted in Miss Pinney's description, the plasmasome does not appear until after synizesis is established. Some of the nuclei figured by Foot and Strobell would seem to be presynizetic in development and could not therefore contain plasmasomes.

I would conclude, therefore, that after synizesis there are present in the first spermatocyte nuclei two nucleolus-like bodies, one the accessory chromosome and the other a plasmasome. Further, that the accessory chromosome exists throughout the whole period, for a time, as a short, heavy thread, at other times concentrated into a mass, and finally in the late prophases as a straight longitudinally split rod. The plasmasome, on the other hand, is an inconstant structure, absent before synizesis, and again in the late prophase, and is not to be mistaken for the accessory chromosome.

5. *What is the behavior of the accessory chromosome in the first spermatocyte mitosis?*

Reference has already been made to the condition of the accessory chromosome in the late prophase and to its position in the equatorial plate. It appears in the metaphase as a univalent, longitudinally split rod lying outside the ring of ordinary chromosomes. In division its halves separate and during the anaphase move to the two poles of the spindle as do those of the other chromosomes. Examples of this may be seen in figures 2, 3, 4, 5, 6, 7, 8, 9, 10, plate LXXI. Both series of daughter chromosomes may be seen in plate LXXI, figure 3, which shows a mid-anaphase with the halves of the accessory chomosome accompanying each group. There appears to be no question on the part of anyone regarding the movements of the chromosomes in the first spermatocyte, so that an extended discussion on this point is not called for.

From the fact, however, that Foot and Strobell have used the tardy division of the accessory chromosome in the first spermatocyte as an argument to prove its division in the second spermatocyte, because here also it lingers for some time near the equatorial plate after the other chromosomes have moved toward the poles of the spindle, it will be necessary to call at-

tention to figures 6, 7, 8, 9, 10, plate LXXI. These show that while the time of division is later than that of the other chromosomes the actual separation occurs and the halves of the divided accessory chromosome may, in each case, be seen in the daughter cells. No instance could be observed where there could be doubt of this fact. The clearness of these phenomena is due to the fact that the accessory chromosome remains, as in the prophase, distinct from the other chromosomes, so that it can be followed even into the telophase. As will be seen later, the same aloofness on the part of the accessory chromosome is encountered in the second spermatocyte and is so marked that there is no difficulty in tracing its behavior.

6. *What is the behavior of the chromosomes in interkinesis?*

The interval between the two spermatocyte divisions is comparatively brief and the changes in the relative positions of the chromosomes slight. While the chromosomes mass together, the outlines of the individual elements may be seen clearly in favorable preparations of the telophase. Since the whole daughter chromosome complex travels to the pole at about the same rate, its members at the end of the movement lie at approximately the same level. When therefore the second spermatocyte spindle is formed there is little or no change in the positions of the chromosomes, and the equatorial plate of the metaphase corresponds in general with that of the first spermatocyte, from which it was derived. While this is true, the slight movements of all the chromosomes during their poleward migration usually results in a destruction of the typical ring arrangement so characteristic of the first spermatocyte. Because of its isolated position and somewhat greater variation of movement in the anaphases, the accessory shows more marked differences in position in the equatorial plate than the other chromosomes. If it has moved toward the pole at the same rate as the rest of the complex and maintains its position during the telophase it will then be found upon the periphery of the equatorial plate in the second spermatocyte. If, on the contrary, as often happens, the movement is slightly slower than that of the other chromosomes and it swings around under the mass during the anaphase movements it will later appear within the group of chromosomes in the resulting equatorial plate. It is not possible, therefore, to recognize the ac-

cessory in the second spermatocyte by its position, as might frequently be done in the first spermatocyte. I am of the opinion accordingly that any identification based upon position alone is not warranted in the case of the accessory chromosome in the second spermatocyte. By this I do not mean that there may not be similar arrangements of the chromosomes in both spermatocyte metaphases, but rather that the opportunities for movements of the chromosomes during the first spermatocyte anaphase and telophase are so great that no rule may be laid down to mark a type of second spermatocyte. (Plate LXXI, figures 11, 12.)

7. *What is the behavior of the accessory chromosome in the second spermatocyte mitosis?*

At this point in the history of the accessory chromosome of *Anasa* there occurs the wide diversity of opinion between Foot and Strobell and the other investigators who have studied it. The issue is clearly drawn. Foot and Strobell claim that the accessory chromosome is divided in the second spermatocyte as in the first spermatocyte, but Wilson and others are just as positive that it passes undivided into but one of the pair of spermatids formed by the division of each second spermatocyte. Issues are joined here on a question of fact, and it becomes necessary to determine, therefore, whether the accessory chromosome divides in the second spermatocyte metaphase or whether it passes undivided into one of the two daughter cells.

I must confess that it is a matter of no little astonishment to me that there should be any difference of opinion on this point, because the conditions are so clear and unmistakable as almost to preclude error. A number of photomicrographs of the second spermatocyte anaphase have been prepared from both sections and smears and are reproduced in plate LXXI, figures 13-27. In figure 15 there are shown ten pairs of spermatids as they appeared spread upon the glass slip. This slide was prepared according to the method of Foot and Strobell and shows the cells practically separated so that there can be no question of a later division of the accessory chromosome. In each one of these ten pairs it is clearly seen that one member contains an accessory chromosome while its mate lacks it. The same statement holds true of all similar cells drawn and photographed, and of the thousands of others examined. *In no case*

was a divided accessory chromosome found in any second spermatocyte. For a short time the accessory chromosome lies against the mass of chromosomes, but when the spermatids are separated and the nuclei re-form it moves away again and lies at one side. Such conditions are shown in plate LXXI, figures 20-21, 25-27. No clearer or more precise demonstration of a cytological fact could be asked than is here afforded by the unilateral movement of the accessory chromosome.

The question naturally arises, why, if this be true, should two observers decide that the accessory chromosome *does* here divide? It is of course, impossible to explain just why this has occurred, but it would seem to me that Foot and Strobell were impressed with the necessity of showing every chromosome in both daughter cells and that they chose stages which exhibited such arrangements. Since it is impossible to find these conditions after a mid-anaphase, owing to the massing together of the chromosomes, all their pictures were made in the early anaphase while the accessory chromosome lies in or near the equatorial plate. *Not a single photograph of an unmistakably completely divided second spermatocyte is shown among all their figures.* Since it is only at this time that the accessory chromosome may definitely be demonstrated to occur in only one daughter cell their failure to figure it may be understood.

Since Foot and Strobell base their case upon the evidence afforded by their photographs, it is proper that these should be considered. They show in plate III twenty-three figures of second spermatocyte anaphases and telophases. In all but figure 45 the accessory chromosome lies undivided in the equatorial plate, and in this two independent nuclei with no clearly marked accessory chromosomes are advanced as evidence that the accessory chromosome has divided. Figure 46 shows also two nuclei with no indication that they are daughter derivatives. Figures 29, 30, 31 and 44 are introduced to show the actual division of the accessory chromosome. Figure 29 shows the accessory chromosome of a mid-anaphase with a slight constriction at the center, figure 30 a similar cell with two distorted and ill-defined chromosome masses, figure 31 two other similar daughter groups with an apparently divided lagging chromosome, while figure 44 exhibits a mid-anaphase with the daughter (?) groups widely separated and turned by spread-

ing and a broken accessory chromosome midway between them. In all of these cells the chromosomes are thin and of indefinite outline and have apparently suffered much in the process of preparation. There is not a clear case of a divided accessory chromosome in the series, although individual cells, doubtless the best that could be found, are selected and photographed. That later stages show conclusively the undivided accessory chromosome, not alone in selected cases but in every cell in a microscopical field, is demonstrated in plate LXXI, figure 15, of this paper.

The objection may be raised that such a stage does not show all the chromosomes; but it is not a valid objection because it is impossible to photograph all the chromosomes at this stage on account of their apparent fusion into a mass. Moreover, the essential facts are admitted by all. It is agreed that all the chromosomes, with the exception of the accessory chromosome, divide so that each group contains ten ordinary chromosomes; it is agreed that the lagging chromosome is the accessory chromosome. The question therefore to be answered concerns the behavior of the lagging chromosome. Are its derivatives found in each of the separated daughter cells of the second spermatocyte; or is it, undivided, included in only one of the two? The evidence on both sides has been presented in statement, drawing, and photograph and the judgment of those interested must, in the absence of personal study, be based upon the presentations. The crux of the situation lies here, for if the accessory chromosome divides there is no dimorphism of the spermatozoa and no visible sexual differentiation of the paternal germ cells, but if it remains undivided then there is a dimorphism of the spermatozoa and a consequent visible chromosome differential between two numerically equivalent classes.

It is pertinent to consider also whether in evaluating the evidence in this case, any considerable number of genuine instances of unusual conditions can be held to invalidate the common conclusions reached by numerous independent students of these phenomena. There can be no question of the occurrence of abnormal conditions in the development of the germ cells. Entire cysts, or even testes, become degenerate from imperfect coördination in development; certain daughter

groups of cells fail to separate and thus produce spermatids with two or four tails and as many simplex groups of chromosomes; minor aberrations occur throughout all stages. Can these be held to prove that there is no constancy in the processes and results of spermatogenesis? Can deviations from the normal or average be regarded as an argument against a type? If so there can be no general laws in biology.

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CONTENTS:

FOUNDATIONS OF ARITHMETIC..... *Arthur Bowes Frizell.*

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THE FOUNDATIONS OF ARITHMETIC.

DISSERTATION FOR THE DEGREE OF DOCTOR OF PHILOSOPHY, SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL OF THE UNIVERSITY OF KANSAS.

BY ARTHUR BOWES FRIZELL, OF BOSTON.

This thesis seeks a foundation for arithmetic in the ideas underlying Cantor's formulation of his system of ordinal types.

It proceeds by postulating, but follows D. Hilbert and G. Peano rather than E. V. Huntington. The search is for postulates possessing heuristic and didactic, not merely subsumptive value.

A *motif* is found in the notion of an abstract group, which secures the development step by step of all number systems so far studied without further postulates than those needed for the transfinite ordinals.

As axioms are to be avoided, it is necessary to state carefully the definitions and theorems used even when they are well known to the mathematicians, but in this case the proofs are omitted.

1. *Definition.* A set of symbols $a, b, \ldots$ will be said to form a K-class if we possess a test which enables us to assert in every case either that $a = b$ or that a is not $= b$ subject only to the restrictions that

a) the result of comparison be uniquely determined
b) the statements $b = a$ and $a = b$ shall be interchangeable
c) from $a = b$ and $b = c$ must follow $a = c$
d) $a = a$ if K contains no other symbol equal to a.

2. *Definition.* An infinite set of symbols is one which contains parts that can be put into one correspondence with the whole. A finite set is one that is not infinite.

3. *Definition.* An ordered set is one in which we are always able to say either that a precedes b $(a < b)$ or that a follows b $(a > b)$ subject only to the restrictions that
a) the result of comparison is uniquely determined
b) $a < b$ shall exclude $a = b$ but involve $b > a$
c) if $a < b$ and $b < c$, then $a < c$
d) if $a' = a$ and $b' = b$, then $a' < b'$ or $a' > b'$ according as $a < b$ or $a > b$.

4. *Definition.* An ordered set is said to be well ordered when it has a first element and every subset beginning with the first element has an immediate successor in the given set.

5. *Definition.* A procedure whereby to every a, b of a K-class is assigned a definite symbol $c = a \circ b$ will be called a C-rule or rule of combination provided that by this assignment equals with equals give equals.

6. *Definition.* A K-class is said to possess the fundamental group property with respect to a C-rule when $a \circ b$ also belongs to K.

7. *Definition.* Modulus of a K-class with regard to a C-rule is a symbol u of K such that $a \circ u = a = u \circ a$ for every a in K.

8. *Proposition I.* An ordered set defined by the requirements: **a**) it shall contain a given symbol e; **b**) it shall possess the group property for every combi-

nation $e \circ a$ where a denotes a previously defined member of the set is also well ordered, infinite and forms a K-class with respect to the given rule. *Proof:* By hypothesis the set is to contain $e \circ e = e'$, $e \circ e' = e''$, $e \circ e'' = e'''$, . . . Since it is to be an ordered set no two of its members can be equal $\therefore$ to every element of the whole set can be assigned some one of the subset e', e''', e^v, . . . That is, the set is infinite. And by **b**) every element has an immediate successor. Finally we have a test for equality which satisfies the requirements of § 1.

9. *Scholium.* A set defined as in § 8 contains no modulus. In what follows it will be referred to as an e-set.

10. *Postulates.* We postulate an e-set for a lower rule of combination which shall contain a lower symbol u and e-sets for both this and a higher rule which shall both contain a higher symbol w, the definitions of the rules of combination to be completed in §§ 17, 26, 28, 30.

11. The different sets $\mathrm{K}[u \circ]$, $\mathrm{K}[w \circ]$, $\mathrm{K}[w \square]$ are to be so ordered that the lower shall precede the higher. Thus they form together a well ordered set

u, $u \circ u = u'$, $u \circ u' = u''$, $u \circ u'' = u'''$, ...

w, $w \circ w = wu'$, $w \circ wu' = wu''$, $w \circ wu'' = wu'''$, . . .

$w \square w = w^{u'}$, $w \square w^{u'} = w^{u''}$, $w \square w^{u''} = w^{u'''}$, . . .

12. *Postulates.* We postulate e-sets for the lower rule which shall contain respectively each of the symbols $w^{u'}$, $w^{u''}$, $w^{u'''}$, . . . in succession. Thus corresponding to every a of the set $\mathrm{K}[w \square]$ we shall have an e-set $\mathrm{K}[a \circ] : a$, $a \circ a = au'$, $a \circ au' = au''$, . . . Now taking *e. g.* $a = w^{u'''}$, by the principle of § 11 every member of $\mathrm{K}[w^{u'''} \circ]$ precedes $ww^{u'''} = w^{u^{iv}}$ and therefore falls between $w^{u'''}$ and $w^{u^{iv}}$. That is, all these new e-sets are interpolated between successive

elements of $K[w\square]$. Hence the totality of symbols forms a well ordered set.

13. *Proposition II.* A rule of combination is associative throughout a given K-class if

$$a\circ(b\circ c)=a\circ b\circ c$$

for every a, b, c in K.

14. *Definition.* A K-class is said to form a semigroup with regard to a C-rule associative throughout K if by this rule unequals with equals always give unequals or if from the relation $a'\circ b=a\circ b$, resp. $a\circ b'=a\circ b$ we can always infer $a'=a$ resp. $b'=b$.

15. *Proposition III.* No semigroup contains more than one modulus for its defining C-rule. For if u and u' not $=u$ were both moduli, we should have $a\circ u'=a=a\circ u$ contrary to § 14.

16. *Definition.* An abelian K-class with reference to a C-rule is one for which the rule is without exception commutative.

17. *Proposition IV.* Sufficient conditions of an abelian class are the relations

$$a\circ(b\circ c)=a\circ b\circ c \quad \text{and} \quad b\circ a=a\circ b$$

for every a, b, c in the class.

18. *Proposition V.* A C-rule is distributive over another in a given K-class if the relations

$$(a\circ b)c=ac\circ bc \quad \text{and} \quad a(b\circ c)=ab\circ ac$$

are satisfied by every a, b, c in K.

19. *Proposition VI.* A necessary and sufficient condition of the generating rule of an e-set being associative for the set is the inductive formula of definition.

$$e\circ a\circ b=e\circ(a\circ b).$$

Proof. If the relation of $a\circ(b\circ c)=a\circ b\circ c$ has been established for a certain a and every b, c of the set, then by hypothesis $e\circ a\circ(b\circ c)=e\circ\{a\circ(b\circ c)\}=e\circ\{a\circ b\circ c\}=e\circ(a\circ b)\circ c=e\circ a\circ b\circ c$.

But $e \circ b \circ c = e \circ (b \circ c)$ by definition.

Therefore $e' \circ b \circ c = e' \circ (b \circ c)$ and so on.

Hence the theorem by strict induction.

20. *Corollary.* The rule is also commutative. For if $e \circ a = a \circ e$, then by the associative law $e \circ a \circ e = e \circ (a \circ e) = e \circ (e \circ a)$. But $e \circ e' = e' \circ e$ by § 19, therefore $e \circ e'' = e'' \circ e$, and so on. And if $b \circ a = a \circ b$ for a certain a and every b then $b \circ (e \circ a) = b \circ (a \circ e) = b \circ a \circ e = a \circ b \circ e = e \circ (a \circ b) = e \circ a \circ b$.

Hence the proposition follows by strict induction.

21. *Proposition VII.* The formula of § 19 is also a sufficient condition of the e-set constituting an abelian semigroup for its generating C-rule. *Proof.* If $a \circ b$ belongs to the given e-set, then $e \circ a \circ b = e \circ (a \circ b)$ also belongs to it. Thus the first group property is established. We have proved the associative law and by definition no two numbers of the set are equal. Therefore $a' \circ b$ is not $= a \circ b$ when a' is not $= a$.

22. *Postulates.* Using capital letters M, N, ... to denote elements of the lowest class K$[u \circ]$, and italic letters a, b, . . . for those of the class K$[w \square]$ where a shall precede b, we postulate for every $MB = BM$ a set $MB \circ Na$ for every Na, then using letters a, b, ... where a shall precede b to denote the resulting symbols we postulate inductively new sets b $\circ$ a where a $= Na$ and b denotes successively the higher "polynomial" or composite symbols. Every b-set is to be simply ordered and possess the first group property for every b $\circ$ a.

23. *Proposition VIII.* Every b-set is well ordered, infinite and forms a K-class for the rule denoted by $\circ$. For the b-set consists of the combinations b, b $\circ$ a, b $\circ$ a u', b $\circ$ a u'', b $\circ$ a u''', ... and the reasoning of *Prop. I* holds good.

24. *Proposition IX.* The b-sets belonging to a

given Mb form together an infinite, well ordered K-class as regards the rule $\circ$. For the set of b's:

$$Mb,\ Mb \circ w^{(n)},\ Mb \circ w^{(n \square u)},\ \ldots\ .$$

forms a well ordered K-class between consecutive members of which the b-sets are interpolated.

25. *Proposition X.* The totality of the b-sets forms an infinite, well ordered K-class as regards the rule $\circ$. For the set of Mb belonging to a given b is a well ordered K-class and so is the whole set of b's, the latter being simply $K[w\square]$.

26. New combinations of symbols already defined are defined inductively in accordance with the formulas

$$b \circ a = a \circ b \qquad \text{and}$$
$$a \circ (b \circ c) = a \circ b \circ c.$$

This secures the group property for the whole set and the reasoning of *VI* and *VII* establishes

Proposition XI. The set of symbols generated according to two rules, a higher and a lower, from a single arbitrary symbol w by aid of the postulate of order, the restricted form of the group property and the above inducted formulas of definition, is a well ordered, infinite set constituting an abelian semigroup with regard to the lower rule.

27. *Scholium.* The higher rule remains unrestricted and has not been defined beyond the set $K[w\square]$, therefore is not yet a C-rule for the K-class of § 26.

28. *Definition.* The higher rule shall be defined inductively throughout $K[w\square]$ by the formula

$$w\,a\,b = w \square a\,b,$$

where a, b are any members of $K[w\square]$ for which $a\,b$ has already been defined.

29. *Proposition XII.* The class $K[w\square]$ forms an abelian semigroup with regard to its generating rule. Proof by *Propositions VI* and *VII.*

30. *Definition.* The higher rule shall be defined inductively for the remaining symbols of our abelian semigroup on the lower rule according to the formulas

$$(a \circ b)c = ac \circ bc \text{ and } a(b \circ c) = ab \circ ac,$$

where the combinations ab, ac, bc shall have been already defined.

31. *Proposition XIII.* The higher rule is distributive over the lower throughout the class of symbols defined in § 22. *Proof.* First let $a = b = c = l$ where l is any symbol of $\mathrm{K}[w \square]$. Then ll is defined by § 28 and $l(l \circ l) = ll \circ ll = (l \circ l)l$ by § 30. Now suppose that the formulas of § 30 have been established for all symbols of $\mathrm{K}[l \circ]$ up to and including a certain a and for every b and c.

Then
$$\begin{aligned}(l \circ a \circ b)c &= \{l \circ (a \circ b)\}c \text{ by associative law,}\\ &= lc \circ (a \circ b)c \quad \text{by hypothesis,}\\ &= lc \circ (ac \circ bc) \quad \text{by hypothesis,}\\ &= lc \circ ac \circ bc \quad \text{by associative law,}\\ &= (l \circ a)c \circ bc.\end{aligned}$$

Similarly in every other case when a, b, c are replaced by $l \circ a$, $l \circ b$, $l \circ c$ respectively. But by definition $l(l \circ \mathrm{N}a) = ll \circ a \square \mathrm{N}a$ and so on. Therefore by strict induction the formulas hold for every a, b, c belonging to the same $\mathrm{K}[l \circ]$. Hence by *Prop. V* the theorem is true in this case. If h, k, l denote different members of $\mathrm{K}[w \square]$ the definition gives

$$(h \circ k)l = hl \circ kl \text{ and } h(k \circ l) = hk \circ hl.$$

Then the proof is completed inductively by the same reasoning as above.

32. *Corollary 1.* The higher rule is a C-rule and by it unequals with equals give unequals. For since our symbols form a well ordered set according to the lower rule, we have $\mathrm{a} = \mathrm{b} \circ \mathrm{x}$ for any two unequal elements a, b and therefore $\mathrm{ac} = \mathrm{bc} \circ \mathrm{xc}$ $\therefore$ not $= \mathrm{bc}$.

33. *Corollary 2.* The higher rule is associative.

For this property has been established for the elements a, b, ... as members of K[w □]. Therefore by the distributive law it holds generally.

34. *Corollary 3.* The higher rule is commutative. For this also has been proved in the class K[w □].

35. *Corollary 4.* The set of symbols defined in § 22 forms an abelian semigroup with reference to the higher rule.

36. *Scholium.* Beginning with any $a > w$ we have abelian semigroups with regard to both rules, and so beginning with w for one or the other rule, but no part beginning with w forms a semigroup on both rules.

37. *Proposition XIV.* Necessary and sufficient conditions that a set M constitute an abelian semigroup with respect to each of two rules of combination, one distributive over the other, that M contain an arbitrary w and that M be as generated an ordered set, are the rules of combination thus far defined.

38. *Corollary.* The properties in question may be expressed by the following postulates:

A. There shall be a higher and a lower rule of combination.

B. Combinations of symbols shall be so ordered that those made by the lower rule precede combinations of the same symbols by the higher.

C. The higher rule shall be distributive over the lower.

D. There shall be a set M containing the symbol w.

E. M shall form an abelian semigroup for the lower rule.

F. M shall form an abelian semigroup for the higher rule.

G. Every successive set generated according to requirements shall be an ordered set.

39. *Scholium.* M is a well ordered set with no modulus.

40. We postulated two rules of combination for the symbol w, but only one for the lower symbol u. If we should postulate a higher rule for u by the same requirements as for w the resulting set of symbols would not differ as regards any group property from the w-set; the new abelian semigroups would be respectively holoedrically isomorphic with the former. If we postulate no higher rule the set $K[u\circ]$ still forms an abelian semigroup holoedrically isomorphic with $K[w\circ]$.

41. Instead let us set up postulates for the u class of symbols differing from those of § 38 only in adding another postulate H. The symbol u shall be a modulus for the higher rule, with the restriction on A–G that they shall not conflict with H. Then the class $K[u\square]$ reduces to the single element u, the abelian semigroup on the two rules reduces to the set $K[u\circ]$ and postulate B drops out, since every combination by the higher rule is found among those made according to the lower rule. This new set of postulates may be replaced by the equivalent set.

42. **a.** There shall be a higher rule defined from a lower by the inductive formulas $(u\circ a)^b = u^b \circ a^b$ and $a(u\circ b) = au\circ ab$.

b. There shall be a lower rule defined inductively by the formula $u\circ a\circ b = u\circ(a\circ b)$.

c. There shall be a set M containing the symbol u.

d. The set M shall possess the group property for every combination $u\circ a$.

e. M shall be an ordered set.

f. There shall be a set M′ built up by postulates c, d and e on the symbol uu.

g. The sets M′ and M shall be identical.

43. *Proposition XV.* The set of symbols defined by the above seven postulates constitutes an abelian semigroup for each rule and has a modulus for the higher rule, which is distributive over the lower.

Proof. The abelian semigroup on the lower rule is established by *Prop. VII*, the distributive law follows from XIII and the other semigroup by § 35. It remains to prove the existence of a modulus.

Let $e = uu$. By postulate g, e must occur in the set $K[u\circ] : u, u', u'', \ . \ . \ .$

Suppose $e = u''$. Then every member of $K[e\circ]$ will be found in $K[u\circ]$ but beyond u'. That is, u and u' are not in $K[e\circ]$, contrary to g. Therefore the only possibility of satisfying g is $e = u$. Since, then, $uu = u$, it follows by the distributive law that u is a modulus.

44. Postulates a . . . g define the natural numbers as ordinal symbols and by *XV* contain all the laws of their arithmetic. The cardinal numbers may be defined in a manner now familiar as names of classes, *e. g.*, "five" is the name given to the class of all well ordered sets which are ordinally similar to the set u, u', u'', u''', u^{iv}.

45. *Definition.* A group is a semigroup which contains, corresponding to every a, b, in it, symbols p and q such that $a\circ p = b = q\circ a$.

46. *Proposition XVI.* Every group contains a modulus with respect to its defining C-rule.

47. *Definition.* If a class which has a modulus u for its defining C-rule contains symbols a, $\bar{a}$ such that $a\circ\bar{a} = u = \bar{a}\circ a$ then a, $\bar{a}$ are said to be each the *inverse* of the other.

48. *Proposition XVII.* No member of a semigroup can have more than one inverse in the semigroup. For otherwise equals with unequals would give equals.

49. *Proposition XVIII.* Every group contains the inverse of every one of its members.

50. *Proposition XIX.* A semigroup with modulus is a group if it also contains the inverse of every one of its members.

Proof. $a \circ (\bar{a} \circ b) = a \circ \bar{a} \circ b = u \circ b = b$, and $(b \circ \bar{a}) \circ a = b \circ (\bar{a} \circ a) = b \circ u = b$, that is, § 45 is satisfied by $p = \bar{a} \circ b$ and $q = b \circ \bar{a}$.

51. *Proposition XX.* Given an abelian semigroup G with reference to a rule denoted by $\circ$, if in the class $[(m, n)] = C$ of pairs of elements of G we declare $(m, q) = (n, p)$ when and only when $m \circ p = n \circ q$ and set up a rule defined by the relation $(m, q) \odot (n, r) = (m \circ n, q \circ r)$, then 1) C will be a K-class, 2) $\odot$ a C-rule, 3) C an abelian group as regards the rule denoted by the sign $\odot$.

Proof. 1) Either $m \circ p = n \circ q$ or $m \circ p$ is not $= n \circ q$ by hypothesis and § 1. Hence either $(m, q) = (n, p)$ or (m, q) is not $= (n, p)$. Obviously the assertions $(n, p) = (m, q)$ and $(m, q) = (n, p)$ are identical in meaning, since this is so for $n \circ q$ and $m \circ p$. It remains to verify the euclidean postulate.

Suppose that $(m, q) = (l, r)$ and $(l, r) = (n, p)$.

Then $m \circ r = l \circ q$ and $l \circ p = n \circ r$.

Hence $(m \circ r) \circ (l \circ p) = (n \circ r) \circ (l \circ q)$.

But since G is an abelian semigroup $(m \circ r) \circ (l \circ p) = m \circ r \circ l \circ p = (m \circ p) \circ (l \circ r)$ and likewise $(n \circ r) \circ (l \circ q) = (n \circ q) \circ (l \circ r)$. Therefore $(m \circ p) \circ (l \circ r) = (n \circ q) \circ (l \circ r)$. Whence $m \circ p = n \circ q$ by definition of semigroup and finally $(m, q) = (n, p)$ by definition of equality.

2) Let $(m', q') = (m, q)$ and $(n', r') = (n, r)$. Therefore $m' \circ q = m \circ q'$ and $n' \circ r = n \circ r'$. Whence as under 1) $(m' \circ n') \circ (q \circ r) = (m \circ n) \circ (q' \circ r')$ and hence $(m' \circ n', q' \circ r' = (m \circ n, q \circ r)$. That is $(m', q') \odot$

$(n', r') = (m, q) \odot (n, r)$, or equals by equals give equals and $\odot$ denotes a C-rule.

3) The fundamental group property is secured by the definition. To prove the associative law we have $(m, n) \odot \{(p, q) \odot (r, s)\} = (m \circ p \circ r, n \circ q \circ s) = (m, n) \odot (p, q) \odot (r, s)$. Suppose that $(m', q') \odot (n, r) = (m, q) \odot (n, r)$. Then $(m' \circ n, q' \circ r') = (m \circ n, q \circ r)$ by definition. Hence $(m' \circ n) \circ (q \circ r) = (m \circ n) \circ (q' \circ r)$ and $(m' \circ q) \circ (n \circ r) = (m \circ q') \circ (n \circ r)$. Therefore $m' \circ q = m \circ q'$ by § 14. That is $(m', q') = (m, q)$ and similarly for the other form of this property. Thus C is a semigroup. But the element (m, m) is a modulus and to every (n, q) corresponds an inverse (q, n). Therefore by *XIX*, C is a group, which we will denote by G.

Finally $(n, r) \odot (m, q) = (n \circ m, r \circ q)$
$= (m \circ n, q \circ r) = (m, q) \odot (n, r)$.

Therefore by § 16, G is an abelian group.

52. The semigroup C and group G are connected by *Proposition XXI.* If we declare $(m \circ q, q) = m$ then $(m \circ q, q) \odot (n \circ r, r) = m \circ n$. For $(m \circ q, q) \odot (n \circ r, r)$ $= (m \circ q \circ n \circ r, q \circ r) = m \circ n \circ q \circ r, q \circ r) = m \circ n$.

53. *Scholium.* The group G contains a semigroup K holoedrically isomorphic with C in such manner that the rule $\odot$ becomes identical with the rule $\circ$ for K.

54. Obviously *Prop. XX* may be applied to the set of natural numbers in two different ways according as we use the semigroup on addition or that on multiplication. An essential distinction between these two procedures is furnished by

55. *Proposition XXII.* Given two rules of combination of which one is distributive over the other, no set of symbols can form a group with respect to both rules. For such a set would contain a modulus v for the lower rule (*XVI*). Then by the distributive law

$a = bx = b(x \circ v) = bx \circ bv = a \circ bv$ for every a. That is bv is also a modulus. But there can not be more than one modulus (*III*). Therefore $bv = v$ for every b so that when b' is not $= b$ we have $b'v = v = bv$ contrary to definition.

56. *Corollary.* It is not possible to define a set of symbols constituting a semigroup with modulus as regards both rules of § 55.

57. If *Prop. XX* is applied to the set of natural numbers and the rule of addition, we lose the semigroup on multiplication and can not recover it. This semigroup, in fact, is destroyed if we only annex a modulus for addition. Consequently we give the preference to the semigroup on multiplication and proceed with the group G obtained by applying *XX* to it.

58. *Proposition XXIII.* Given a higher rule distributive over a lower, and a set of symbols forming an abelian semigroup with respect to each rule, if we build the group G of § 52 with reference to the higher rule, then a necessary and sufficient condition of having a lower rule over which the higher shall be distributive and with regard to which G shall constitute an abelian semigroup is the formula of definition $(m, q) \circ (n, r) = (mr \circ nq, qr)$.

Proof. The necessity of this relation is obvious. To show that it is sufficient we first let $(m', q') = (m, q)$ and $(n', r') = (n, r)$ $\therefore (m'q = mq')$ and $n'r = nr'$. Therefore $m'r'qr = m'qrr' = mrq'r'$ and $n'q'qr = nqq'r'$. Hence $(m'r' \circ n'q)qr = (mr \circ nq)q'r'$ by distributive law and $\therefore$ by definition $(m'r' \circ n'q'q'r') = (mr \circ nq, qr)$ or equals with equals give equals and we have a C-rule. Similarly equals with unequals give unequals. For the associative law $(k, l) \circ \{(m, q) \circ (n, r)\} = (k, l) \circ (mr \circ nq, qr) = (kqr \circ lmr \circ lnq, lqr) = (kq \circ lm, lq) \circ (n, r) = (k, l) \circ (m, q) \circ (n, r)$.

Obviously $(n, r) \circ (m, q) = (m, q) \circ (n, r)$. Thus we have an abelian semigroup and the distributive principle follows by taking equals with equals.

59. *Definition.* The symbols of G shall be ordered according to the convention that (m, q) shall precede or follow (n, q) according as m precedes or follows n and by § 3.

60. *Scholium.* If a, b denote two natural numbers that have no common factor other than unity, the set of symbols (a, b) is simply ordered by the above definition. This set, which we will denote by R, may be taken as representative of G since every element of G is equal to some member of R.

61. *Definition.* The symbols constituting the set R are called absolute, rational numbers.

62. *Proposition XXIV.* Every two unequal elements of G are connected by a relation $h = g \circ x$ where h, g denote the given elements, g being that which precedes.

For $g = (m, q) = (mr, qr)$ and $h = (n, r) = (nq, qr)$ and mr precedes nq by hypothesis. Therefore $h = g \circ x$ is satisfied by $x = (d, qr)$ where $nq = mr \circ d$.

63. *Corollary.* The set R is simply ordered according to the lower rule denoted by $\circ$.

64. *Proposition XXV.* If we exclude the modulus u the remaining symbols of R form a set which is simply ordered according to the higher rule. For let x denote any element of R which precedes and y any one which follows u.

Then gx precedes and gy follows g. That is, the trios u, g, gx and u, g, gy are ordered whether g precedes or follows u.

65. *Corollary.* The modulus u separates the remaining symbols of R into two simply ordered classes, neither of which contains either a first or last element.

66. It is possible to divide R into two ordered classes so that every element of R belongs either to the one or to the other, but neither class has either a first or a last member. For example, the class R_1 of all elements whose squares precede 2 and the class R_2 of all whose squares follow 2 together exhaust the set R, while neither R_1 nor R_2 has either a first or a last element. If we take 4 instead of 2, the element 2 is not included either in R or in R_2; it separates them. We usually make this separation in practice by selecting a well ordered set, *e. g.* according to the decimal scale. We take first the highest integer in R_1, then the highest number of tenths, hundredths and so on. Similarly we pick out first the lowest integer in R_2, then the lowest set of tenths, hundredths, etc.

67. *Definition.* A well ordered set which has no last element is called a series.

68. *Definition.* The series of all symbols of the well ordered set $1, 2, \ldots w, w+1, \ldots 2w, \ldots 3w, \ldots w^2, \ldots$ which precede the element a taken in the above order, is said to be a series of type a.

69. *Definition.* An ordered set which has no first nor last element will be called an unbounded set.

70. Given an unbounded set S ordered according to a rule with respect to which S constitutes an abelian semigroup, suppose that a series $K[f_n]$ of type w has been selected from among the elements of S and let W_1 denote the set of all symbols of S which follow, V_2 all which precede every f_i, let V_1 denote the set of all symbols s which precede W_1 and W_2 the set of all that follow V_2.

Then one of the sets W_1, V_1 must be unbounded and both may be. So also of V_2 and W_2.

71. In every one of the four cases when
W_1 has a first element or V_1 has a last
V_2 has a last element or W_2 a first
this element is called the limit of the set to which it belongs.

72. In case W_1 and V_1 or V_2 and W_2 are both unbounded we will introduce a new symbol f_w which we will call the limit of $K[f_n]$.

73. *Lemma.* If W_i and V_i are both unbounded for the series $K[f_n]$ the same is true for the series $K[a \circ f_n]$ where a is any symbol in S. For if either the W or V set corresponding to $K|a \circ f_n|$ had a limit l we could write $l = a \circ x$ and x would be a limit for the same W or V belonging to $K|f_n|$ contrary to hypothesis.

74. *Theorem.* If the series $K|f_i|$, $K|g_j|$ both divide S into two unbounded sets the same is true of the set $K|f_i \circ g_i|$.

Proof. Let $h_1 = f_1 \circ g_1$, $h_2 = f_2 \circ g_2$, ...
$h_{w+1} = f_2 \circ g_1$, $h_{w+2} = f_2 \circ g_2$, . . .
$h_{2w+1} = f_3 \circ g_1$, $h_{2w+2} = f_3 \circ g_2$, . . .

Then by the Lemma each of the series $K[h_j]$, $K[h_{w+j}]$, $K[h_{2w+j}]$, . . . $K[h_{iw+j}]$, . . . divides S into two unbounded sets. Hence the same is true of the set h_1, h_{w+2}, h_{2w+3}, . . . h_{iw+i+1}.

75. On the basis of the preceding theorem and definitions is built up, by laying down the usual definitions of equality, order and two rules of combination, the set X of limits of series $K[f_n]$ selected out of R. The set X forms an abelian group with reference to the higher rule of combination and an abelian semigroup on the lower rule. The higher rule is distributive over the lower and possesses the modulus u. X may be simply ordered according to the lower rule and is divided by the modulus u into two unbounded sets each

simply ordered according to the higher rule. X is itself an unbounded set and contains a sub set holoedrically isomorphic with R as regards each rule of combination. Thus the whole set of absolute numbers is deduced from the set of absolute rational numbers by using only principles of order.

76. The preceding development does not take account of the possibility that $K[f_n]$ may not really divide S. There may be no symbol which follows every f_i. Then W_1 is an empty class and V_1 is taken to coincide with S. Thus if $K[f_n|$ and $K[g_n|$ are both series of this kind, they both have the same W and V, whence if new symbols f_w, g_w were to be introduced the principle of definition used in § 75 would lead us to declare $f_w = g_w$. Therefore we assign to the totality of the sets $K|f_n|$ for which W_1 is an empty class a single symbol Z which is to follow every element of X. Then following § 75, $Z \circ g_w$ is to be defined as h_w where $h_n = f_n \circ g_n$ and $f_w = Z$. But for $K[h_w|$, W_1 is empty, therefore $Z \circ x = Z \circ g_w = h_w = Z$. That is, $Z + x = Z = x + Z$, $Zx = Z = xZ$, and similarly $Z + Z = Z = ZZ = Z^3 = Z^N$. The associative, commutative and distributive laws still hold as well as the first group property, but the semigroup is destroyed for both rules by violating the law of equals with unequals.

77. It is also possible that no symbol in S precedes every f_i. Then V_2 is an empty class and W_2 coincides with S. On the same principle as in § 76 we assign to the totality of series of this kind a single symbol v to precede every x and define $v \circ x = h_w$ where $h_n = f_n \circ g_n$, $g_w = x$, $f_w = v$. And now the two rules must be distinguished. Since no x precedes every f_i the sets $K|f_n + g_n]$ and $K[g_n|$ separate S into the same V and W. Therefore $v + x = h_w = g_w = x + v$. And for the same reason no s can precede every $f_n\, g_n$

$$\therefore \quad vx = (fg)_w = v = xv$$

Also in like manner $v + v = v = vv$.

In the set $K[h, v]$ the associative, commutative and distributive laws and the first group property are all preserved. The law of equals with unequals is violated for multiplication but still holds for addition, for which v is a modulus.

78. Since the introduction of infinity would destroy both semigroups while zero destroys only that on multiplication, it seems preferable to admit zero to our arithmetic and exclude infinity. But this removes the only objection to enlarging the addition semigroup into a group. This is effected at a stroke by applying *Prop. XX* to the set X and thus building an abelian group with reference to addition. In this group we then define a higher rule by the formulas

$$\bar{a} \odot b - \overline{ab} = a \odot \bar{b} \text{ and } \bar{a} \odot \bar{b} = ab.$$

This completes the system of real numbers, forming an abelian group on addition and, when we exclude its modulus, an abelian group on multiplication, which is distributive over addition. The system of real numbers can be simply ordered according to the lower rule, but the abelian group on the higher rule can not be similarly treated.

79. We might have proceeded by first applying XX to the natural numbers as a semigroup on addition. This yields the whole set of integers, positive, negative and zero. Omitting zero and defining by the law of signs we should have an abelian semigroup on multiplication. Applying XX to it, there results an abelian group composed of all rational numbers except zero. Then the introduction of the limits would supply the whole set of irrational numbers and close by reintroducing zero.

80. As long as we postulate two rules of combination, one distributive over the other, and demand semi-

groups with reference to both, we are led inevitably to the transfinite types in case we impose no restriction on the multiplication table and, if we require a modulus, to the natural numbers, whence the system of real numbers results from the attempt to build groups. The two rules of combination connected by the distributive property may be regarded as defining arithmetic up to date; it has not yet been found profitable to postulate in any other way. Then transfinite arithmetic is distinguished by postulating the semigroups and finite arithmetic by the postulate of the modulus.

81. The real numbers form the most general finite system with a single unit and must enter into every system with more than one principal unit, one unit must always be the modulus. Systems with two or more principal units have been studied exhaustively by Weierstrass. Here the abelian group on the lower rule is postulated universally.

With two principal units, if we exclude the modulus of the lower rule, the necessary and sufficient condition of an abelian semigroup on the higher rule is the existence in the system of a symbol i such that $ii = \bar{u}$. Thus the common complex numbers form the most general system with two principal units satisfying the postulates for real members.

82. Within the system of common algebra are distinguished different number bodies each built on a root of a given algebraic equation as a unit. The algebraic numbers of a given body form an abelian group on addition and, excluding zero, an abelian group on multiplication, and must contain a given symbol, the root of the given algebraic equation. For example the system of common complex numbers is the number body which contains a root of the quadratic $x^2 + 1 = 0$.

83. An integral algebraic number satisfies an equation

$$x^N + a_1 x^{N-1} + \ldots + a_i x^{N-i} + \ldots + a_n = 0,$$

where every a_i is an integer. A good illustration of the serviceableness of the group theory process for arithmetic is the theorem: The whole numbers of a quadratic number body form an abelian group on addition and, if we exclude zero, an abelian semigroup with regard to multiplication.

84. A more striking illustration is furnished by Dedekinds' "Ideals." An ideal is defined as a combination of the whole numbers of a number body possessing the first group property for both addition and multiplication. The ideals of a given body form an abelian semigroup with respect to multiplication. There is no addition of ideals.

85. Similar applications are found in the expression of an ideal by aid of its basis and in the cognate formulation of the transformations of a collineation in space of N dimensions. The latter question resolves itself into that of complex numbers with N principal units. Here it is no longer possible to preserve even the restricted abelian semigroup on the higher rule.

Not only is the abelian character lost, as in quaternions, but the semigroup property may be violated on account of the possibility of a combination by the higher rule being zero when none of the factors is zero.

86. It is now possible to describe more concisely the relation of the transfinite arithmetic to common arithmetic. The symbols defined in § 22 form a set of numbers with infinitely many principal units w, w^2, w^3, . . *i. e.*, the principal units form a series of type w. In finite arithmetic, it is true, the symbols u^2, u^3, . . . all belong to the set generated from u as principal unit, but if we allow this analogy in the transfinite system there will be still more new symbols.

For just as the removal of restrictions on the higher rule carried our series of symbols beyond the finite set of type w so the introduction of a still higher rule, corresponding to involution, will extend it beyond the set defined in § 22 if we impose no restrictions on the new rule except that of order and the special form of the group property.

87. Let us postulate a rule expressed by a^b higher than the two preceding, that is, the combination a b shall precede a^b. To distinguish we will now call $a\,b$ the lower and $a \circ b$ the lowest rule.

The lower rule has been shown to be associative and commutative for the set $K[w\,\square]$, which forms an abelian semigroup with regard to it. A set of symbols shall be generated from w by the higher rule in accordance with the postulate of order and the restricted form of the group property for w^a, where a is a previously defined element. By Prop. I this set forms a series $w, w^w = w', w^{w'} = w'', w^{w''} w''', \ldots$ and now w' must follow every w^N $(N = 2, 3, \ldots)$ [w^N is not a combination by rule, the N is a mere index]. Then by § 22 we obtain a series holoedrically isomorphic with the set there considered if to the lowest and lower rules respectively we make the lower and higher correspond.

88. The articulation of the two lower rules in §§ 28–35 leaves room for much freedom in definition. There we defined the lowest rule first and made the lower depend upon it. Here we have already defined the lower rule to the extent implied in the application of § 22. This, however, involves no further restriction than the inductive associative formula of § 19. But the definition from the lowest rule carries this property with it.

It is therefore permissible to define the lowest rule so that the lower shall be distributive over it. Then by the process of § 22 new combinations are made by the higher and lowest rule together, from each series

of type w in the present set of symbols a new set of the same type as that in § 22. And all new series being fitted in by the nature of the process between consecutive elements of the series previously defined we have at every stage a totality of symbols forming a series.

89. The group properties of the two lowest rules are preserved throughout the preceding process. On every new symbol not obtained from the preceding by postulating them is built up a set forming abelian semigroups on both the lower and lowest rules, the new symbol playing the part of a unit precisely like w in the series of § 22, and in this set the lower rule is distributive over the lowest. This process is to be continued as long as new symbols can be obtained by it.

90. There remains one more possibility of building new symbols by introducing a combination defined one way of the higher symbols with those of the series K $[u \circ]$ according to the lowest rule. Thus to every a in the higher series will be assigned a w-series a, $a \circ u$, $a \circ u'$, $a \circ u''$, $a \circ u'''$, . . .

This series fits in between a and its next following element in the former set so that we still have a totality forming a series.

91. For completeness it is convenient also to define combinations one way of certain symbols with those of K $[u \circ]$ according to the other two rules, viz.: those expressions in which the symbols of K $[u \circ]$ have already been used as marks or indices, *e. g.:*

$u'w$, $u''w$, $u'''w$, . . . $w^{u'}$, $w^{u''}$, $w^{u'''}$, . . .
$u'w'$, $u''w'$, $u'''w'$, . . . $w'^{u'}$ $w'^{u''}$, $w'^{u'''}$, . . .

Expressions $u \circ a$, $u' \circ a$, . . . u'^{w}, u''^{w}, . . . $u'^{w'}$, $u''^{w'}$, . . . are not defined, neither are there any combinations according to the higher rule except the set w^{a} where a belongs to this set. The higher

rule has not been made a rule of combination for any whole set. This would involve assigning properties to it and completing the arithmetic of the symbols we have defined, which is beyond the present purpose. It is enough to have them in series; that forms the foundation of their arithmetic.

92. The mere existence of the series of symbols developed in the preceding §§ is enough to solve a great variety of problems arising in analysis, the nature of which will be illustrated by comparing this series with series consisting of absolute numbers. The natural numbers form a series of type w if they are arranged in the order of their genesis. It is, however, possible to arrange them in series of higher types for *e. g.* the odd numbers alone form a series of type w. If to this we add on the even numbers successively we obtain series of types

$$w+1,\ w+2,\ \ldots\ w+\mathrm{N},\ \ldots$$

and thus the whole set is ordered in type $2w$.

If we order the set R of § 60 as follows:

$$(1,1),\ (2,1),\ (3,1).\ (4,1),\ \ldots$$
$$(1,2),\ (3,2),\ (5,2),\ (7,2),\ \ldots$$
$$(1,3),\ (2,3),\ (5,3),\ (7,3),\ \ldots$$

we have a series which can be put ordinally into one to one correspondence with the series $1, 2, \ldots w+1,\ w+2,\ \ldots\ 2w,\ 2w+1,\ \ldots$ *i. e.*, is of type w^2.

The same set of numbers (the common fractions) can, however, be arranged in a series of higher type. For every finite, simple, continued fraction is equal to some common fraction and conversely. Now let us order the finite continued fractions according to the values of their successive quotients

$$q_1, q_2, q_3, \ \ldots\ q_{\mathrm{N}}.$$

Thus the continued fractions containing each a single quotient form a series of type w. Then from each

member of this series by adding a second quotient results again type w. Therefore the fractions of the form $\frac{1}{q_1+}\frac{1}{q_2}$ may be arranged in series ordinally similar to $1, 2, \ldots w+1, \ldots 2w, \ldots 3w, \ldots$ *i. e.* of type w^2. Annexing a third quotient replaces each element of this set by a series of type w so that we include types w^2+1, w^2+2, $\ldots 2w^2, \ldots 3w^2, \ldots$ *i. e.* the class of fractions $\frac{1}{q_1+}\frac{1}{q_2+}\frac{1}{q_3}$ is ordered in type w^3.

Therefore the whole set of simple continued fractions, comprehending types $w, \ldots w^2, \ldots w^3, \ldots w^N, \ldots$ constitutes, as ordered, a series of type $w^w = w'$.

93. Now it is easy to arrange the natural numbers also in a series of type w' as follows. We know that the class of prime numbers can be put into one to one correspondence with the whole set of natural numbers (the number of primes is infinite).

Therefore we can set up a one to one correspondence ordinally between the prime numbers and the simple continued fractions with a single quotient. By the same reasoning the continued fractions with two quotients are shown to be ordinally similar to the class of product of two primes, *i. e.*, if to every quotient q_1 we assign that prime p_1 for which q_1 is the ordinal number in sequence (so that *e. g.* to the quotient 7 we assign 17) and likewise for a second prime p_2 and quotient q_2, and so on.

Proceeding in this way the class of all products of N primes is exhibited as ordinally similar to the class of continued fractions $\frac{1}{q_1+}\frac{1}{q_2+}\cdots\frac{1}{q_N}$. But the class of all products of primes is the whole set of natural numbers. Therefore by § 92 the natural numbers may be arranged in series w'. Q. E. D.

94. In other words we have here a method whereby

the elements of any w-series may be rearranged so as to produce a series of type w^w. Applying this method successively to the w-series in the preceding we obtain in place of w, $2w$, . . . w', $2w'$ . . . that is, instead of w^2 we get a type ww'. Then w^2+w, w^2+2w, . . . are replaced by $ww'+w'$, $ww'+2w'$, . . . making in all type $2ww'$ replacing the former $2w^2$.

Then come in succession types $3ww'$, $4ww'$, . . . so that the original w^3 expands into a type w^2w'. It is clear that in this way we retrace precisely the steps of the process of § 22, building up on each new symbol the abelian semigroups according to the lower and lowest rules.

Therefore by successive applications of the method it will be possible to rearrange the natural numbers in series of types as high as any of the set hitherto defined. This result may also be stated. The transfinite ordinal series so far defined may each be put into one to one correspondence with the set of natural numbers.

95. The symbols w, $w+1$, $w+2$, . . . *i. e.*, the transfinite symbols, are said to form the second ordinal class, the finite symbols constituting the first class. The latter class was said to be of type w, where w is the symbol following next after all the finite symbols of $K[u\circ]$. Likewise we shall say that the first and second ordinal classes together form a series of type W, introducing this new symbol without assigning to it any properties except that it shall follow next after all symbols of the second ordinal class, *i. e.*, after all the set $K[w^a] : w, w', w'', \ldots$

96. We see that the ordinal symbols play a double role. They were defined as symbols forming a well ordered set. But to each symbol which has no immediate predecessor corresponds a series of which it is the type, viz.: the series of all its predecessors or any ordinally similar series. The arrangements of the nat-

ural numbers in § 94 are only a part of these series. But they are also only a part of the permutations of the whole set of natural numbers. Other permutations are obtained by the following *Lemma.* From any w series of symbols may be obtained a set of permutations of the symbols forming a series of type $w' = w^w$.

Proof. Let a_1, a_2, . . . a_N, . . . denote the given symbols in the given order. Without changing the order of the higher a's put a_1 successively in every subsequent place. This set of permutations is obviously of type w.

From every one of them by repeating the process on a_2 we obtain again a w-series ∴ in all a series of permutations of type w^2. Repeating the process with a_3, a_4, ... successively we have a series of permutations whose type is w'. Q. E. D.

97. Thus the arrangements of the natural numbers furnish a series of type not lower than W. For by § 96 we first deduce from the series 1, 2, 3, ... *i. e.*, the normal order, a set of permutations forming a series of type w'. That is, to every ordinal symbol preceding w' is assigned a permutation, and *vice versa.* Then by § 94 arrange the natural numbers in series w' which obviously is a different permutation from any of the preceding ∵ it can not be obtained by the process of § 96. Now repeating the method of § 96 on each w-series of this permutation we use up all ordinal symbols between w' and that which results from it by a second application of § 94. This holds step by step as long as the latter process can be carried on. Thus to every ordinal symbol in succession preceding W is assigned a new permutation. That is, we have a set of permutations of all the natural numbers forming a series whose ordinal type is W.

98. The process just described for making permutations of all the natural numbers can not yield a series

of type higher than W since, as we have seen, it generates precisely the series W of ordinal symbols. That there are types higher than W is obvious, for we can proceed with W just as with w to generate new e-sets and new abelian semigroups, and there is no limit to the possibilities in the way of still higher symbols and rules. Now it is quite conceivable that there may be further permutations of natural numbers not obtainable by the above process. As a first step toward investigating this question let us consider the simpler one whether the natural numbers themselves can be arranged in a series of ordinal type higher than W. For this purpose we will establish the following

Lemma. Permutations of the natural numbers can be made by the process described and ordered so as to form a series of type higher than any series of all the natural numbers, however arranged. For by the process in question we can always form a new permutation which differs from the first permutation in at least its first element, from the second in at least its second element . . . . . from the $(w+1)$st in at least its $(w+1)$st element, and so on, therefore is not included in any set of permutations ordinally similar to any possible arrangement of all the natural numbers. From this Lemma we readily obtain the

Theorem. Every possible arrangement of the natural numbers is a series of the second class. For by the Lemma to every such arrangement in series can be assigned a set of permutations forming a series of higher ordinal type. But by § 97 the process by which this is effected yields a set of permutations forming a series of type W. Therefore every possible arrangement of natural numbers in series is of type lower than W, therefore belongs to the second ordinal class (being *ipso facto* $\geq w$). Q. E. D.

99. The arrangement of the natural numbers in series of type higher than w finds application in the study of infinite continued fractions. By aid of the euclidean algorithm for greatest common divisor every absolute irrational number less than unity can be expressed as an infinite continued fraction

$$\frac{1}{q_1+}\ \frac{1}{q_2+}\ \cdots\ \frac{1}{q_N+}\ \cdots$$

and conversely. The class of infinite simple continued fractions may therefore be taken as the representative of the class of irrational numbers between zero and 1.

An infinite continued fraction can not be obtained from a finite one merely by annexing quotients; it can only be described by assigning a law which determines q_N for every value of N. An infinite continued fraction may be formed, *e. g.*, by the law that every quotient shall be 2. It is sufficient, however, to consider the class in which the quotients are all different; this can be put into one to one correspondence with the whole class. Accordingly we are concerned with the class of all possible permutations of all the natural numbers. These permutations may be examined in the same way as the permutations of a finite set by imagining a framework of places to be filled, but the number of places is infinite. Moreover, we must provide for the possibility of filling the places in a series of order higher than w. Thus an infinite continued fraction can be formed by filling the even places successively with the odd numbers in their natural order and the odd numbered places with even numbers in the same way, *i. e.*,

$$\frac{1}{2+}\ \frac{1}{1+}\ \frac{1}{4+}\ \frac{1}{3+}\ \frac{1}{6+}\ \frac{1}{5+}\ \cdots\cdots$$

or by filling the odd numbered places with primes and the even places with composite numbers. Or we can select first the places whose indices are primes, then the indices which are products of two primes, three

primes, and so on, and fill these sets with the corresponding sets of numbers permuted in any way we please.

100. We have seen that every possible arrangement of all the natural numbers in a series is of type lower than W. Therefore the quotient places of our framework *in the order in which we propose to fill them* (or rather state how they shall be filled) constitute an ordinal type of the second class. That is, the *numbered places* in a permutation of all the natural numbers, arranged, however, *in the order in which they are to be filled*, form a series obtainable by the process of § 97.* Hence there can be no permutation of all the natural numbers not obtainable by this process, since such a permutation would be *eo ipso* different from all of those hitherto obtained and well ordered in some definite numbered places. In other words, this would mean that the series of the places as they are filled, or the series of numbers with which each place is to be filled, was not obtainable by the process of § 97. Therefore all possible permutations of the natural numbers form a series closely related to the series of type W.

BIOGRAPHY.

I, ARTHUR BOWES FRIZELL, member of the Protestant Episcopal Church, was born in Boston, July 14, 1865. My parents were Joseph Palmer Fessenden Frizell, civil and hydraulic engineer, and Julia Anna (Bowes) Frizell. My early education was chiefly at home and in a private school in Dorchester, Mass. I graduated from the high school in St. Paul, Minn., and spent three years at the Massachusetts Institute of Technology, where I afterwards served as assistant instructor in mathematics, 1888–'91. I received the degree of Bachelor of Arts from Harvard College in 1893 and that of Master of Arts from Harvard University in 1900. I served as instructor in mathematics at New York University 1895–'96, and at Harvard 1897–1906, when I resigned to study abroad. After three semesters at Göttingen, I returned to America, and was appointed, 1908, Professor of Mathematics in Midland College, Atchison, which position I resigned, 1909, to accept an instructorship in the University of Kansas.

*And the preceding statements apply *verbatim* to every series of values admissible in a given numbered place.

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PLATE I.

A. Dakota sandstone resting on Permian shales. Man's head in line with contact. Spring creek, six miles north of Washington.

B. Unconformity of Pleistocene on Permian. Ravine running from left to right in Permian shales with thin limestone forming the top cross a buried gully at right angles to it filled with Pleistocene material which is etching backward. Note the tipping of the limestone into the old gully (undisturbed by recent erosion). About three miles east of Washington.

A

B

PLATE II.

A. Unconformity of Dakota on Permian sandstone at contact projects. Brickyard, east side of Smoky Hill river, Salina.

B. Same. South end of same hill by old mill.

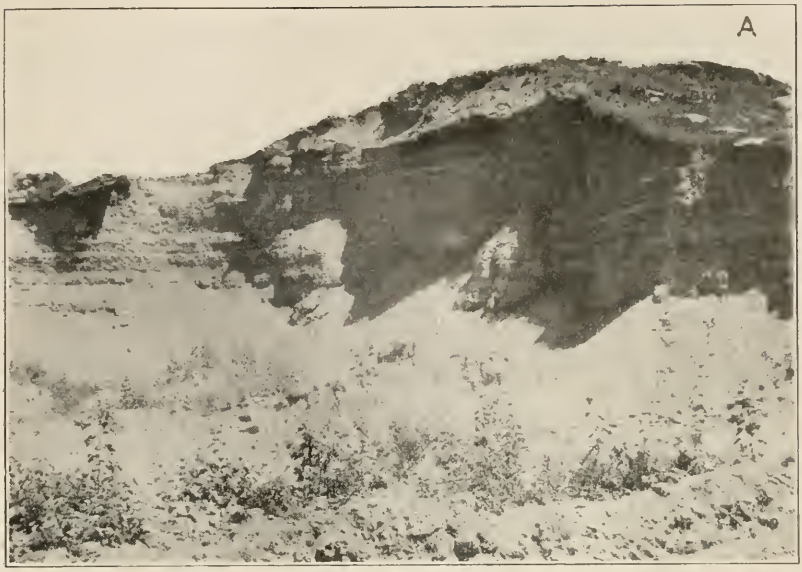
A

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PLATE III.

A. Cliff of Dakota sandstone. East side of Mill creek, northeast of Washington.

B. Slumping of soft sediments, clays apparently of Dakota age. Three miles east of Washington.

A

B

PLATE IV.

A. Slumped soft Dakota clays surrounded by impure sandstone, on Permian floor. Three miles east of Washington.

B. Alfalfa field on the wide terrace of the Republican river, west of Clay Center.

A

B

PLATE V.

FIG. 1.—View looking southwest from ruins, showing heavy ledges of Loup Fork rock in background, from which the pueblo was built. In the foreground two of the party are shown excavating one of the circular pits which occur about twenty yards north of the main building.

FIG. 2.—Ground plan of ruins, showing remains of the division walls, looking west. Remains of the mealing trough shown in the extreme corner of room I, to the left of the observer. To the right, in room V, the small fireplace built into the wall can be seen.

1

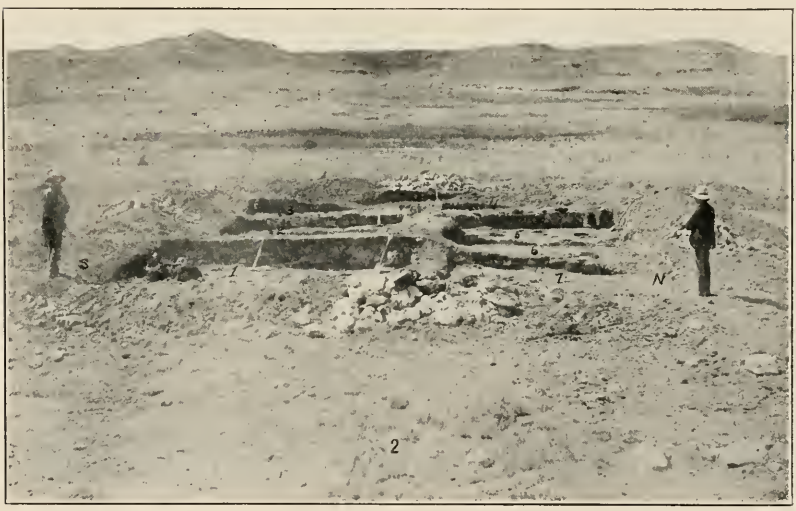
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PLATE VI.

FIG. 3.—Typical Pueblo grinding trough, three feet nine inches long by two feet one inch wide and eighteen inches deep.

FIGS. 4, 5, 6, 7.—Awls or drills, used principally for perforating skins and boring holes into bones, etc. Figure 7 is of a reddish flint, beautifully colored, and of fine workmanship.

FIGS. 8, 9, 10, 11, 12.—Bone implements, probably used to enlarge holes in skins. Have been much used.

FIGS. 13 to 18, inclusive.—Pipes and pipe stems; all are made of native clay. Figure 15 is well made and is decorated with the design shown on plate VIII, figure 62; mouthpiece broken off. Pipe measures two and one-half inches long and seven-eighths inch in diameter at the center.

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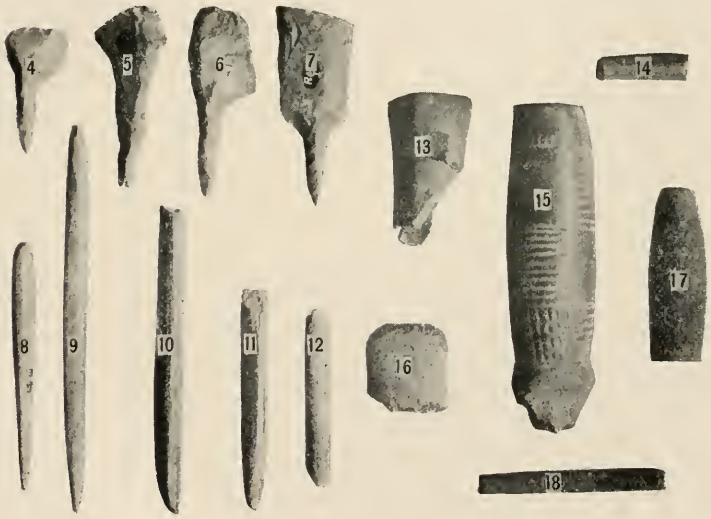
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PLATE VII.

FIGS. 19, 20, 21, 22, 23, 24.—Arrow shaft straighteners. These are made of the Dakota sandstone, and probably came from somewhere in the vicinity of Quivira, for no outcroppings of this material are exposed nearer to Quartelejo than those which occur on the western boundary of Brower's Quivira, about 130 miles east of the Quartelejo pueblo.

FIG. 25.—Bone piccolo, made from the wing bone of a large bird, probably a pelican.

FIG. 26.—Bone implement, possibly a hoe blade, from shoulder blade of buffalo.

FIG. 27.—Tallying implement, made from rib of buffalo.

FIG. 28.—Bone tool with a toothed edge, which may have been used for fleshing skins.

FIG. 29.—Bone tool, made from rib of buffalo, worn smooth and flat, spatula-like.

FIG. 30.—Bone implement of undetermined use, much worn, with toothed edge. Made from shoulder blade.

FIGS. 43 to 56, inclusive.—Fleshers or scrapers, of flint. Figures 43, 45, 46, 47, 51, 52, are beautifully made. Figures 46 and 51 show cross sections of *Fusilina*, a fossil typical of the Carboniferous. The material of these two, at least, is not found in the vicinity of the ruins, and was probably procured from the eastern part of the state.

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PLATE VIII.

FIGS. 57, 58.—Knife blades of yellow chert.

FIG. 59.—One of the most interesting implements found, consisting of the half of an iron ax head, five and one-half inches long by one and a quarter wide at its greatest width, and five-eighths of an inch thick. This, by some mischance, had been split in two longitudinally, and was arranged with a groove around it instead of an eye like our modern axes have.

FIG. 60.—A fine grinder of conglomerate, eleven inches long. Shows much usage.

FIG. 61.—The half of a clam shell, plainly showing saw-tooth marks where it was divided. This was found at the bottom of the twelve-inch hole in room V.

FIG. 62.—Diagram of pattern on pipe bowl shown on plate VI, figure 15. Impression was made on clay and photographed.

FIG. 63.—Base of deer antler, which has evidently been used as some implement.

FIGS. 64 to 69, inclusive.—Specimens of charred corncobs. Figure 59 shows some well-developed kernels on it.

FIG. 70.—Bone implement, well worn.

FIG. 71.—Portion of 'dobe plastering from walls, showing impressions of finger tips.

FIG. 72.—Baked clay marble, evidently used in some game.

FIGS. 73, 74, 75.—Chert scrapers.

FIG. 76.—Hoe blade made from shoulder blade of buffalo.

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PLATE IX.

FIG. 77.—Small metate or grinder, of sandstone.

FIG. 78.—Grinder made of clay mortar and coarse sand, and baked as hard as rock itself.

FIG. 79.—Hammer worked from a glacial boulder; well made and much worn.

FIG. 80.—Grinder, of very fine granite.

FIG. 81.—Grinder, of material same as figure 78.

FIG. 82.—Grinder, made from glacial boulder.

FIGS. 83, 85.—Grinders, of fine sandstone.

FIG. 84.—Knife blade of chert.

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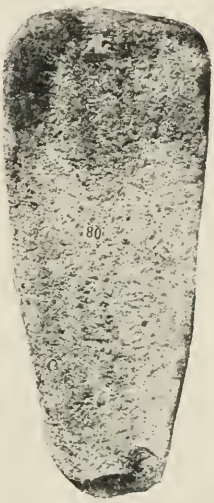
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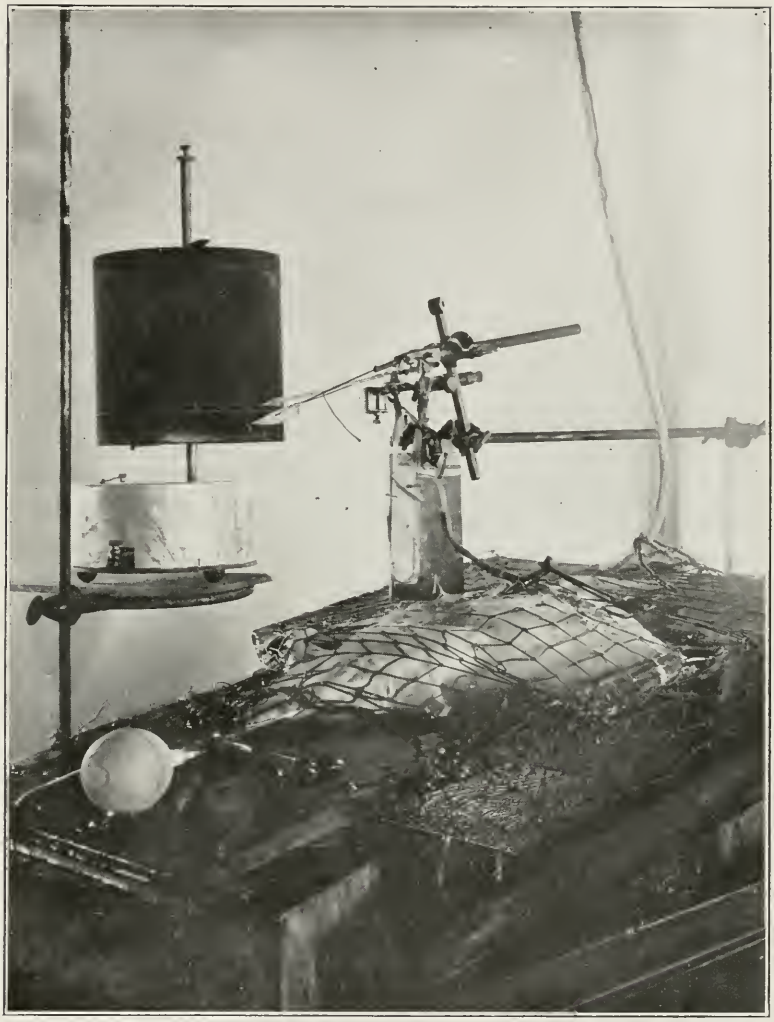

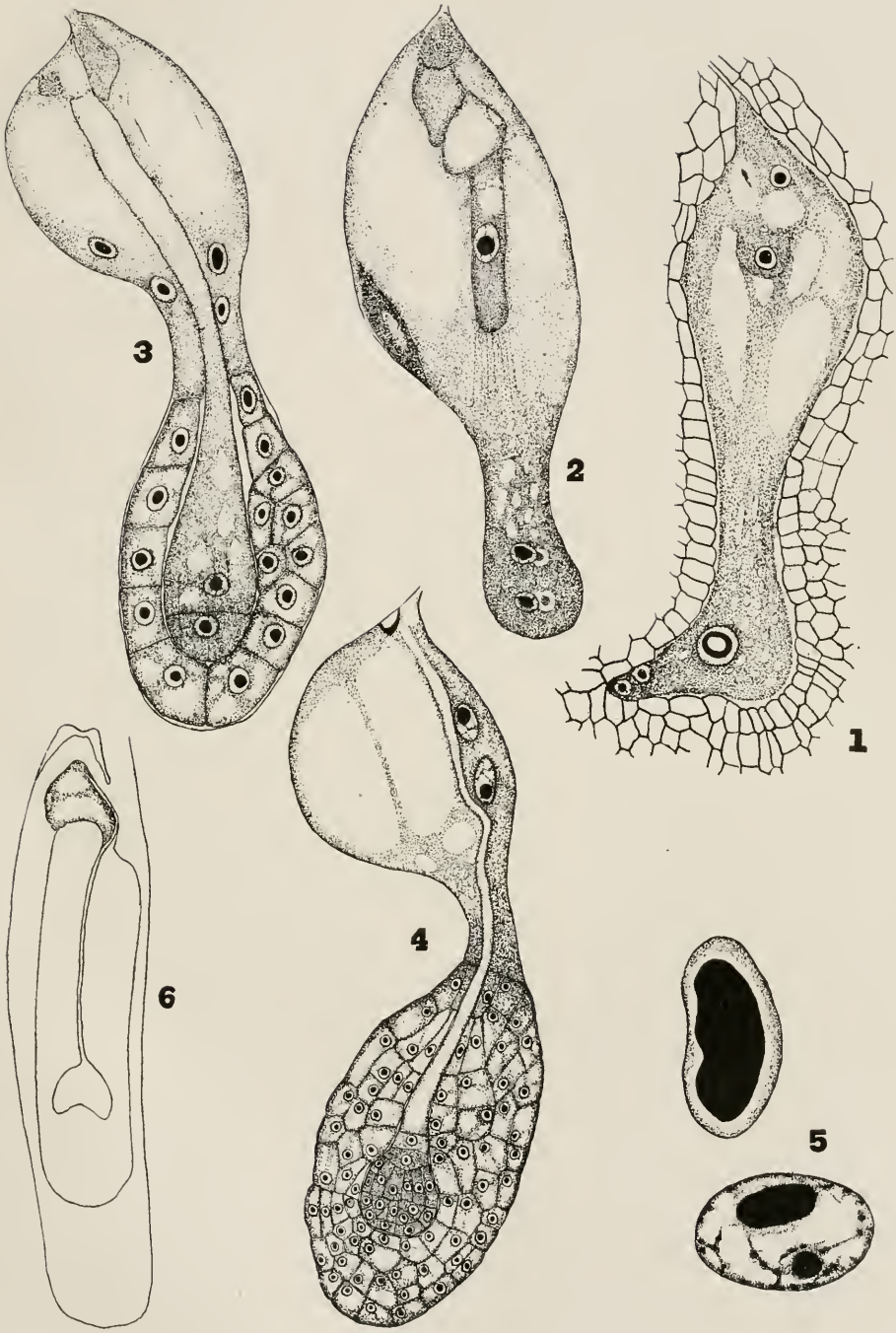
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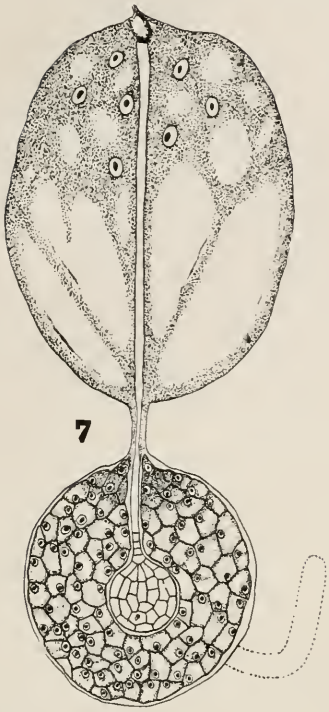

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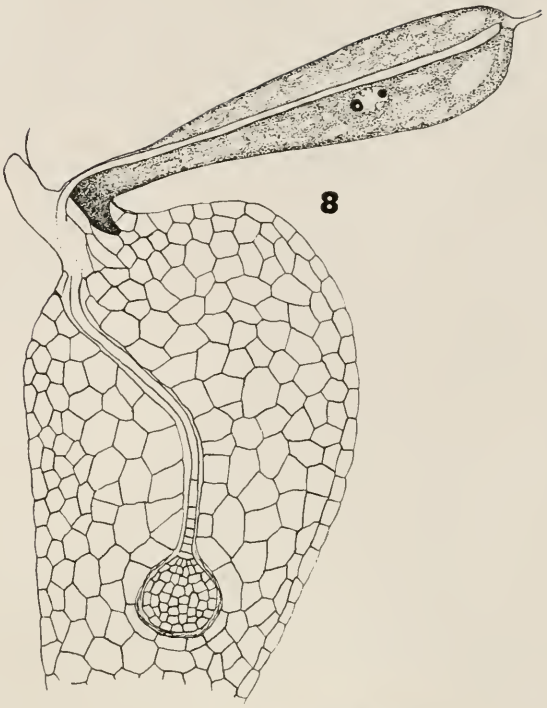

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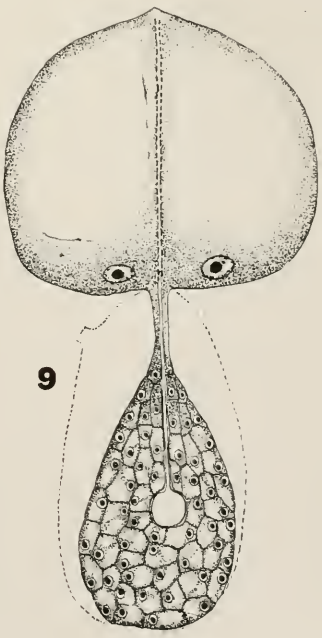

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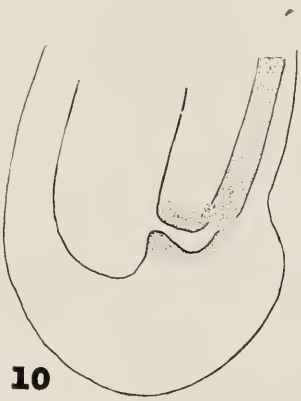

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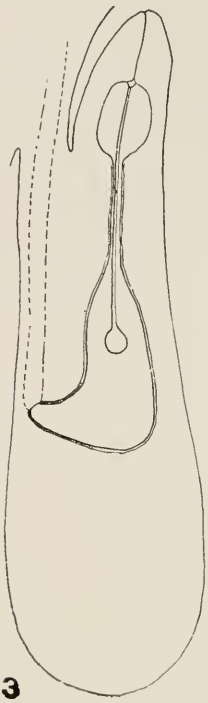

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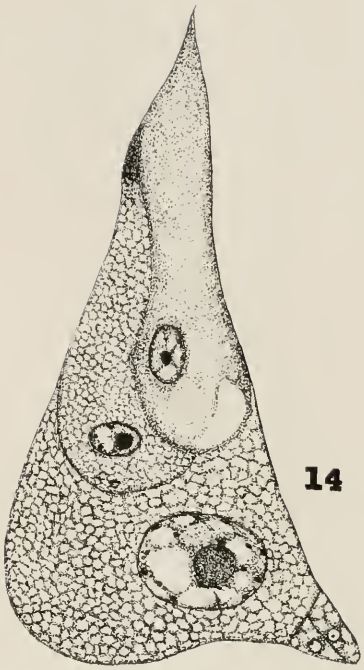

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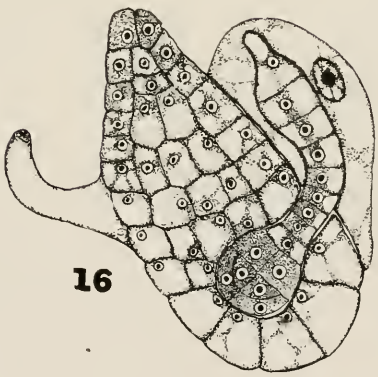

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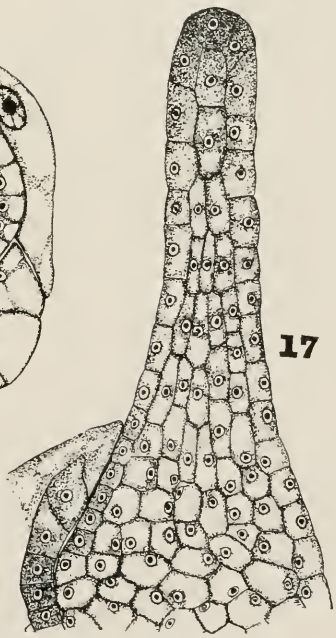

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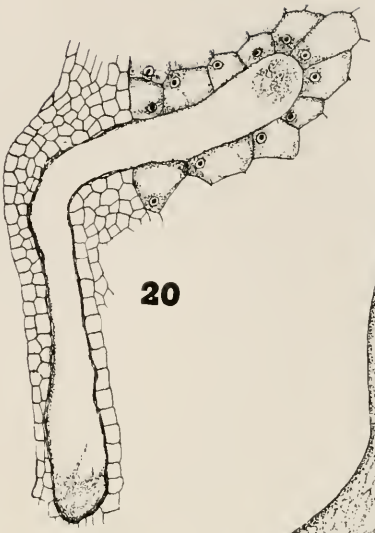

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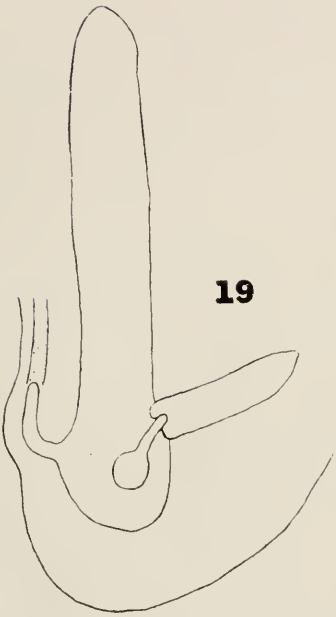

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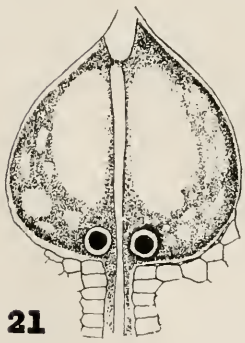

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PLATE XV.

FIG. 1. Two resting cells, showing chromatin granules, and nucleoli with the surrounding clear space.

FIG. 2. Cell beginning mitosis. Close spireme. Nucleoli without the clear space.

FIG. 3. A granular spireme. The nuclear membrane has disappeared but the cytoplasm can still be distinguished from the nuclear sap.

FIG. 4. The chromatin granules are here arranged in rows. This cell has its nuclear membrane yet and the nucleoli have not disappeared.

FIG. 5. Polar view; spireme segmented to form the chromosomes, has a longitudinal split, and is uniformly granular. Nuclear wall just disappeared. Chromosomes looped to form U and J shapes.

FIG. 6. A little later than figure 5. The longitudinal split is very clearly seen.

FIG. 7. Late metaphase. Cytoplasm granular in places, may have been slight plasmolysis in this cell. The spindle fibers are stained very lightly here.

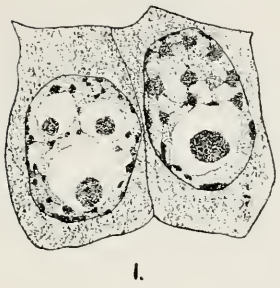
FIG. 8. Metaphase. Spindle shows marked polarity; chromosomes somewhat indefinite.

FIG. 9. Metaphase. Cytoplasm at the ends becoming vacuolated and at the center slightly denser. An especially long chromosome (*m*) is to be noted.

FIG. 10. The cytoplasm of this cell was crushed; however, the chromosomes, which were undivided yet, show the longitudinal split clearly.

FIG. 11. Anaphase. Cytoplasm very granular in places (homogeneous portion not shown). The spindle is well stained in this cell, and the chromosomes have their characteristic bent shape.

FIG. 12. Anaphase. Spindle not clear in this figure. The amount of cytoplasm is small compared to the amount of chromatin here.



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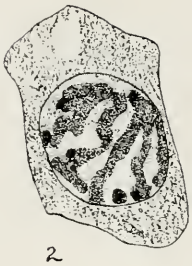

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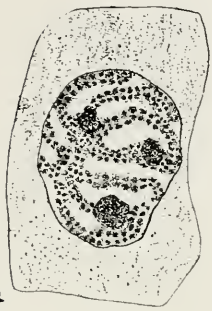

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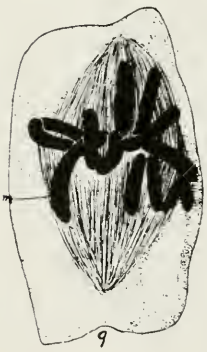

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PLATE XVI.

FIG. 13. Anaphase. Massing of the cytoplasm at the center of the cell.

FIG. 14. Anaphase. The long chromosomes (*m*) are to be seen in this figure.

FIG. 15. Anaphase. Shows relation of chromosomes to spindle during this period.

FIG. 16. Anaphase. Spindle fibers do not show here; reticular cytoplasm (drawn from a slide loaned by Mr. Alban Stewart).

FIG. 17. Anaphase. Polar view; 14 chromosomes.

FIG. 18. Same as 17.

FIG. 19. Telophase. Shows the loosening up of the chromosomes. Cell plate beginning to form.

FIG. 20. Chromatin has diffused throughout the nucleus ahead of the cell-plate formation. A nuclear membrane has also been formed.

FIG. 21. Chromatin a dense mass, very indefinite at the ends of the cell, not shown; cytoplasm much contracted from the cell wall and concentrated about the spindle.

FIG. 22. A very peculiar spindle; cytoplasm much condensed; a second dense spindle formed about the center of the cell where the cell-plate is appearing. Chromatin not shown.

FIG. 23. Concentrated cytoplasm at the spindle center; a very broad spindle and the cell plate extends entirely across it. Cytoplasm vacuolated; the daughter nuclei, not shown in this figure, are nearly reconstructed.

FIG. 24. Cell plate nearly formed; nuclei reconstructed; cytoplasm concentrated at the center. (From slide belonging to Mr. Stewart.)

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PLATE XVII.

Koeberlinia spinosa.

FIG. 1.—Branch of *Koeberlinia spinosa.* × about ½.

FIG. 2.—Aspect of vegetation on mesa near Tucson in the neighborhood from which the specimen was taken.
Photographs by L. M. Peace.

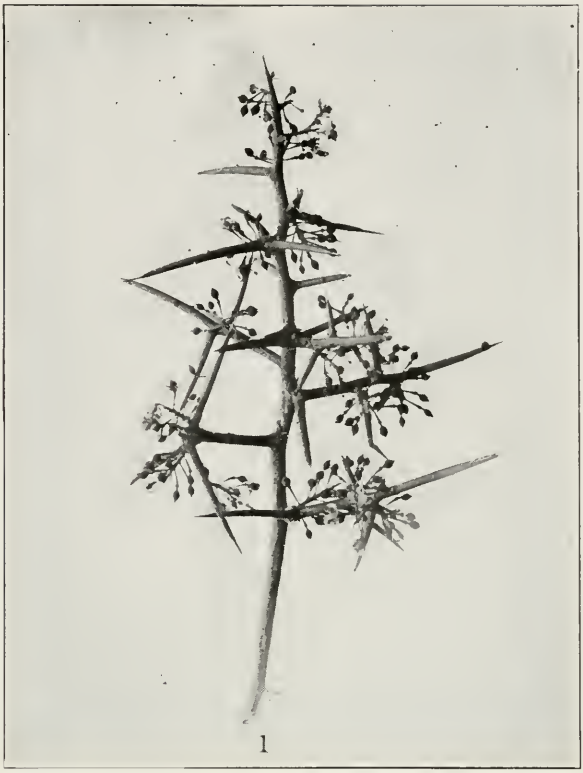

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PLATE XVIII.

Koeberlinia spinosa.

FIG. 1. Cross section of stem. *P*, pith; *M*, medullary ray; *W*, wood; *Tr*, tracheal tubes of year '07 (?); *Ph*, phloëm; *Sa*, spongy parenchyma air space; *Pa*, palisade air space; *Ea*, epidermal air space; *B*, bast; *Scl*, sclerenchymatous tissue. Semi-diagrammatic. × 25.

FIG. 2. (*a*) Section from an older stem, showing traces of annual rings, '07, '05. (*b*) Portion of same stem, opposite side, showing '06 trace. Semi-diagrammatic. × 25.

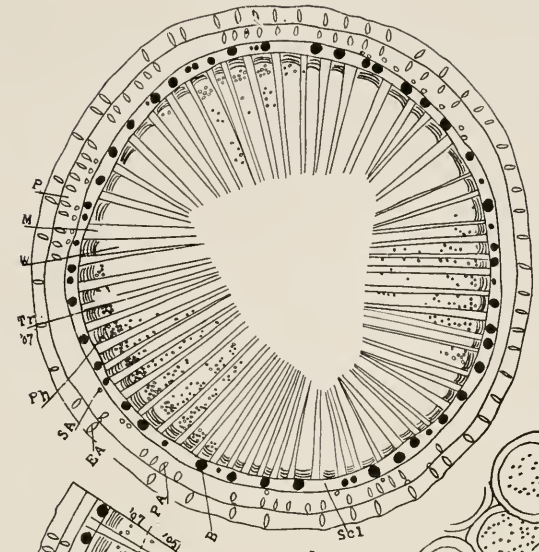
FIG. 3. Cross section of flower branch, showing region of *wa*, water storage cells. × 283.

FIG. 4. (*a*) Pith from flower branch, showing air spaces, *A*. Cross, × 283. (*b*) Single cell from flower-branch pith, showing pits, *P*; air spaces, *A*. Cross, × 400.

FIG. 5. Pith of old stem, showing pitted conditions and starch bodies. Cross, × 283.

FIG. 6. Crystals in old pith cells; longitudinal section. × 283.

FIG. 7. Diagrammatic representation of regions of older stem. *E*, epidermis; *P*, palisade; *Sp*, sponge; *B*, bast; *S*, stone cells; *Ph*, phloëm; *W*, wood. Enlarged.



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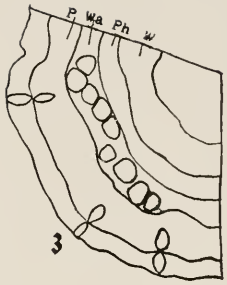

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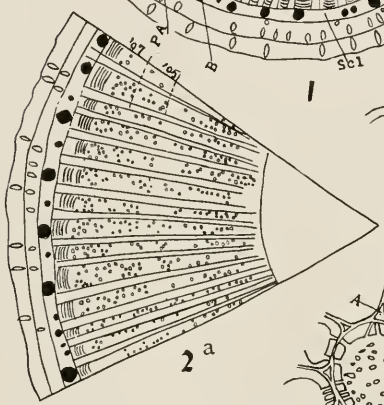

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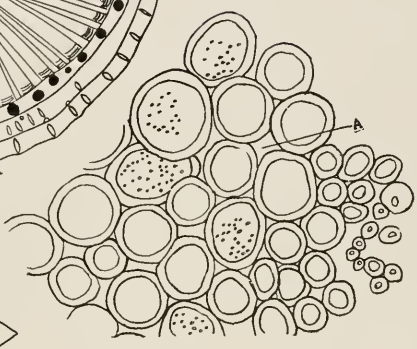

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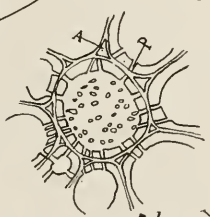

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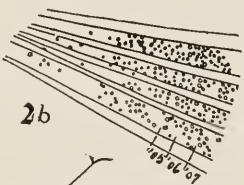

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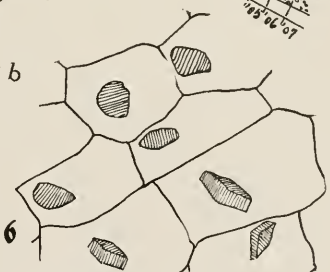

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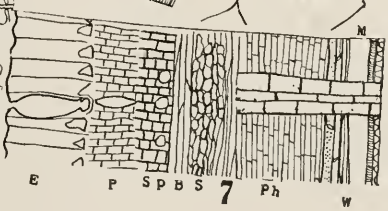

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PLATE XIX.

Koeberlinia spinosa.

FIG. 1. Medullary rays, showing longitudinal extension, longi-tangential section. Semi-diagrammatic. × 55.

FIG. 2. Portion of (1) in detail, showing thick walls, some pits, and numerous aerating places. Tangential. × 283.

FIG. 3. Single medullary ray cell from (2), showing food bodies *F*, *B;* pits, *P;* aerating spaces, *A*. Longi-tangential. × 636.

FIG. 4. Medullary ray cells, showing one elongated and narrow cell *e. c.*, and some more, box-like, for storage, *St.* Longi-radial, × 283.

FIG. 5. Single storage cell from (4), showing food bodies. Longi-radial, × 636.

FIG. 6. Portion of medullary ray extension in phloëm region, showing thin, unpitted walls and cells filled with nitrogenous material. Longi-radial, × 283.

FIG. 7. Portion of older wood, showing tracheids, *Tr;* fiber tracheids, *Ft*, and wood fibers, *wf*. Cross, × 283.

FIG. 8. Detail of (7), showing pitted condition of wood. × 636.

FIG. 9. Water vessels bordering pith. *Tr*, tracheal tubes; *Td*, tracheid; *P*, pith. × 636.

FIG. 10. Spiral tracheids, near pith. Semi-tang., × 283.

FIG. 11. Portion of wood, showing scattered tracheids, *Tr*. Cross, × 283.

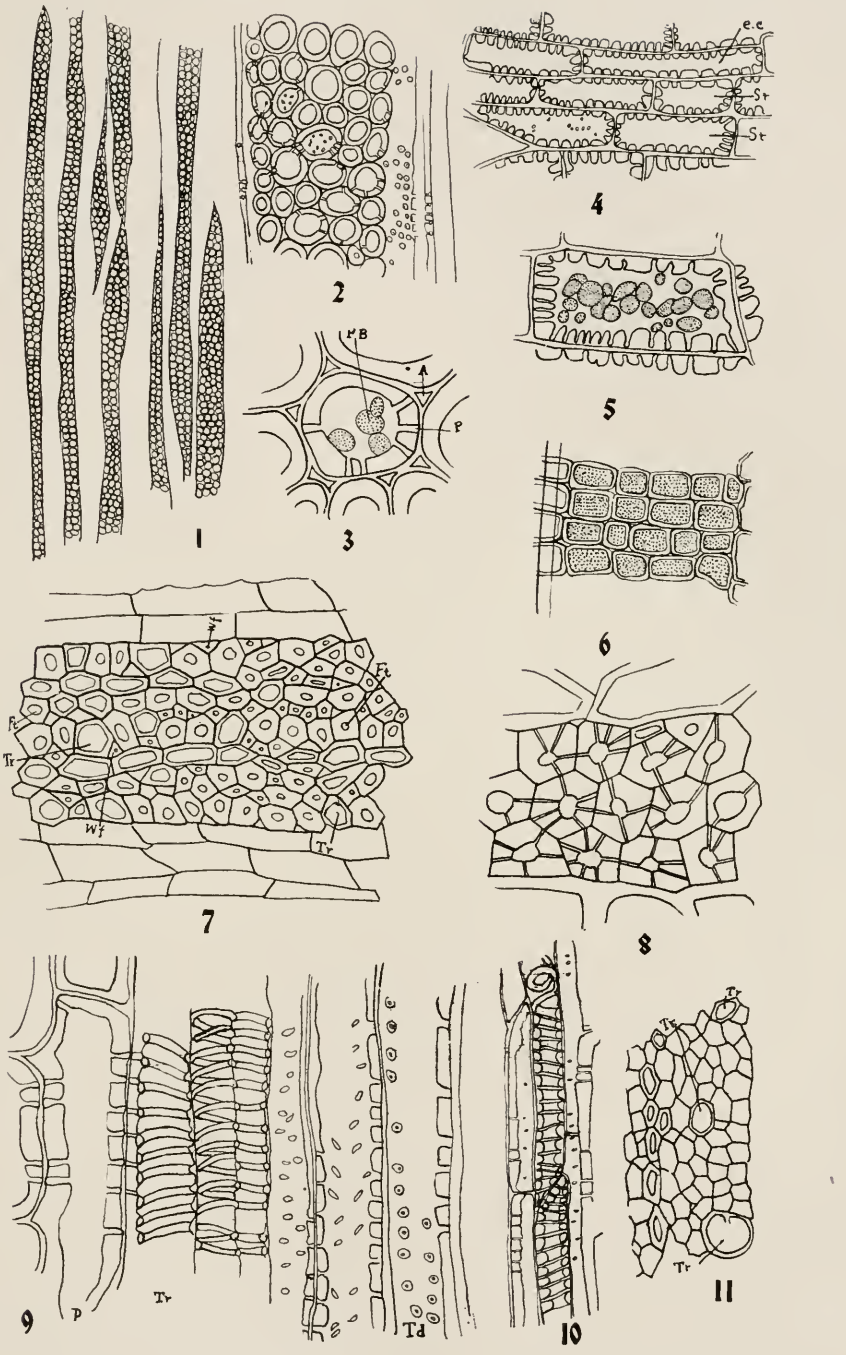

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PLATE XX.

Koeberlinia spinosa.

FIG. 1. Tracheal tube bordering elongated pith cell, on margin of older part of bundle. *P*, pith cell; *Tr*, tracheal tube. Longi-radial, × 636.

FIG. 2. Elongated pith cells densely filled with finely granular food material. Pits in walls omitted. *P*, pith; *W*, wood. Longi-section, × 283.

FIGS. 3, 4, 5, 6. Different views of tracheal tubes, all showing the circular opening at the end. 6 (*a*) Third partition in tube 6, showing section of ring bordering aperture. These have become so completely welded as to give the appearance of a continuous tube, as in 6. Longi-section, × 400. Fig. 3 is the cavity outlined.

FIGS. 7, 8, 9. Sketches showing joining of ends of tracheids. Longi-radial, × 400.

FIGS. 10, 11, 12. Various odd or malformed tracheids. Longi-radial, × 283.

FIG. 13. Regular rectangular tracheids. Longi-radial, × 283.

FIG. 14. Single tracheid. Longi-radial, × 283.

FIG. 15. Fiber-tracheid with small but numerous pits. × 283.

FIG. 16. Wood fiber. Longi-section, × 283.

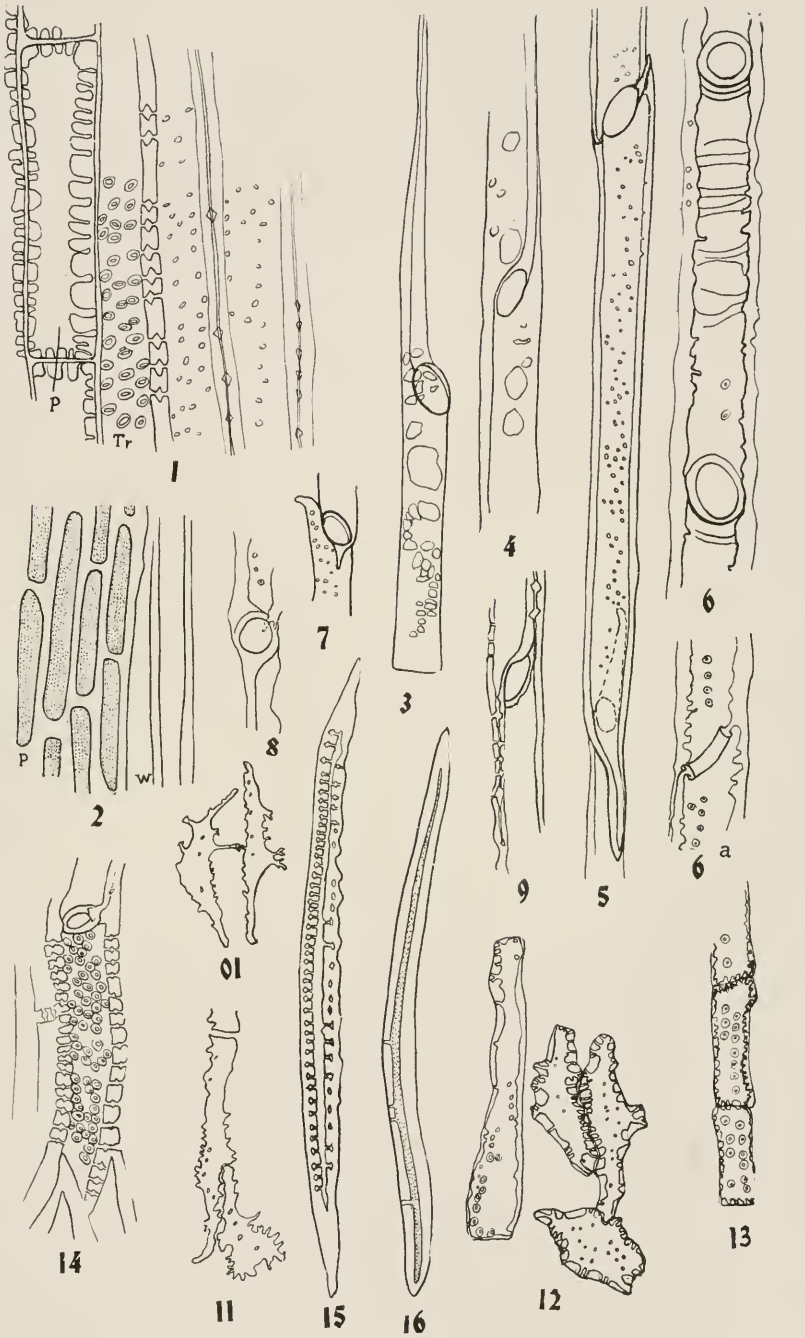
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PLATE XXI.

Koeberlinia spinosa.

FIG. 1. Five rows of phloëm parenchyma cells *p. p.*, as seen in cross section; *m*, medullary-ray cells. × 283.

FIG. 2. Sketch of portion of phloëm, *Ph*, region bordering stone cells, *S*, showing various sizes of cells. Longi-section, × 283.

FIG. 3. Portion of (2) in detail, sieve tubes, *St.*, and sieve plates, *S*, and parenchyma cells alongside, *p*. Longi-section, × 400.

FIG. 4. Stone cells bordering spongy parenchyma, showing some cells unlignified, and some but partly lignified, parenchyma cells; *s*, stone cells; *pc.*, partly lignified; *P*, unlignified. Cross section, × 283.

FIGS. 5, 6. Different sizes and shapes of stone cells. Longi-section, × 283.

FIG. 7. (*a*) Tapering bast fiber. (*b*) Portion of long bast fiber, showing tapering part and projections of wall to support neighboring cells. (*c*) Projections with adjoining cellulose walls in detail. (*d*) Pits in long fiber. All × 283.

FIGS. 8, 9, 10*a*, × 55, 283, 636, respectively. Short bast fibers as they occur securely fastened together. 10*b*, sketch showing pits in short bast fiber, × 636.

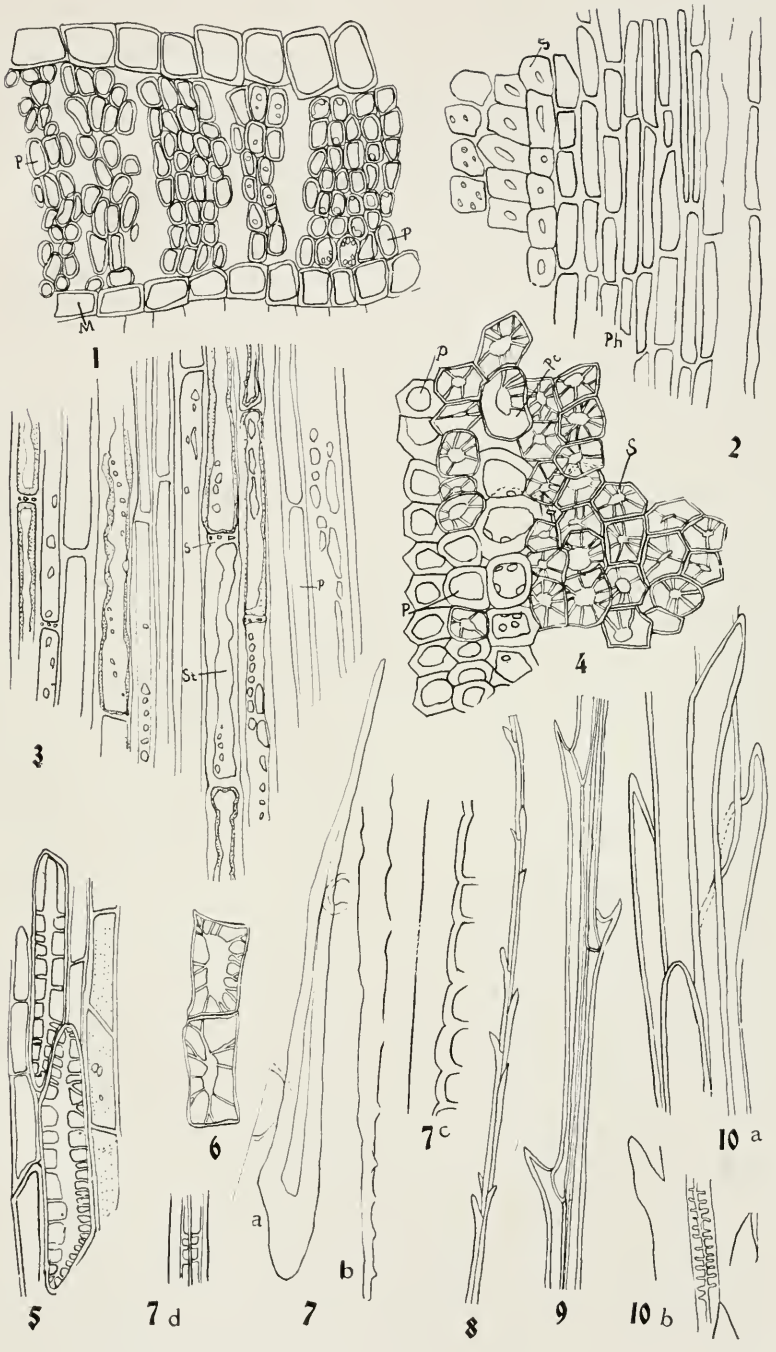
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PLATE XXII.

Koeberlinia spinosa.

FIG. 1. Portion of palisade *P*, and spongy parenchyma, *Sp*, tissue, from stone cells to epidermis. Numerous intercellular spaces *I. S.*, are found. Cross section, × 283.

FIG. 2. End view of palisade cells, showing number and size of chlorophyll bodies. Tangential section, × 283.

FIG. 3. Epidermis of young stem, showing large cellular space, *cs*, and thin walls; this also shows frequency of deeply sunken stomata, *ss*. Cross, × 283.

FIG. 4. Portions of older epidermis, showing reduction of cell space by intense cutinization; cell space, *cs;* cutinized portion, *cp*. Cross, × 283.

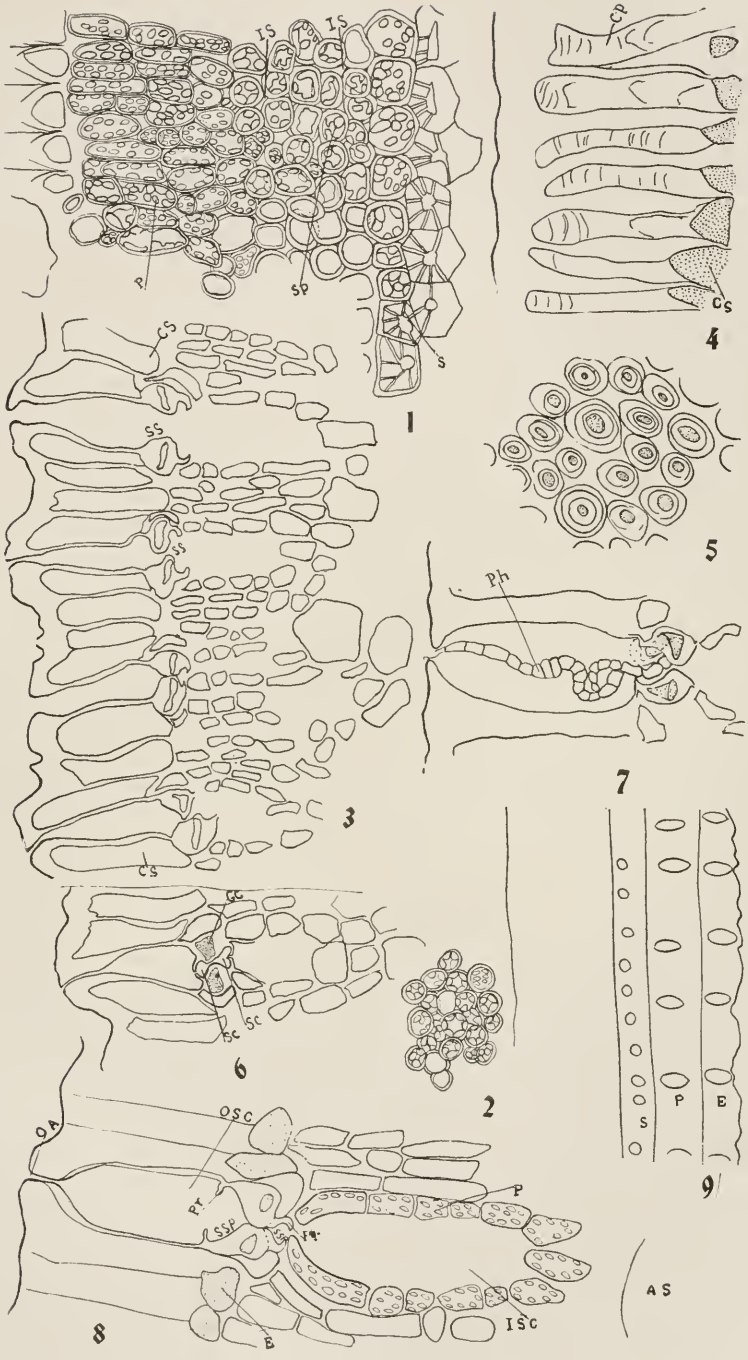
FIG. 5. Tangential view of older epidermal cells, showing thickening of walls. × 283.

FIG. 6. Single stoma from young stem, showing large guard cells, *Gc*. Also, small stomatal chamber proper, above and below, *sc*. Cross, × 283.

FIG. 7. Cuter stomatal chamber invaded by phycomycete, *Ph*. Cross, × 283.

FIG. 8. Stomatal apparatus. *OA, outermost aperture; E*, epidermal cell space; *osc*, outer stomatal air chamber; *isc*, inner stomatal air chamber; *Pr*, projection of thickening, making stomatal spaces proper, *ssp; P*, palisade cells; *AS*, air space in sponge. Cross, × 283.

FIG. 9. Outline of regions of aerating spaces, showing frequency of spaces. *E*, epidermal region; *p*, palisade region; *s*, sponge region. Enlarged.


IS
IS
P
SP
S
1
CS
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SS
CS
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CP
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5
Ph
7
GC
EC
SC
6
2
OA
OSC
PY
SSP
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ISC
8
S
P
E
9
AS

PLATE XXIII.

Koeberlinia spinosa.

FIG. 1. *S*, stone cells filling up lower stomatal chamber; *Ph*, remains of Phycomycete in outer aperture; *d*, portion of "dome." Cross section, × 283.

FIG. 2. Surface view of outer stomatal aperture and epidermal cells. *SA*, stomatal aperture; *EC*, epidermal cells. Tangential section, × 283. Compare with fig. 3, plate XXII.

FIG. 3. View toward outer stomatal aperture from within, showing tips of cells making the "dome." Tangential section, × 283.

FIG. 4. Section across mid-chamber. Tangential, × 283.

FIG. 5. View looking toward stoma, showing shelf, *s*, made by projecting walls. Tangential, × 283.

FIG. 6. Stoma proper, showing guard cells. Tangential, × 283. Compare with fig. 6, plate XXII.

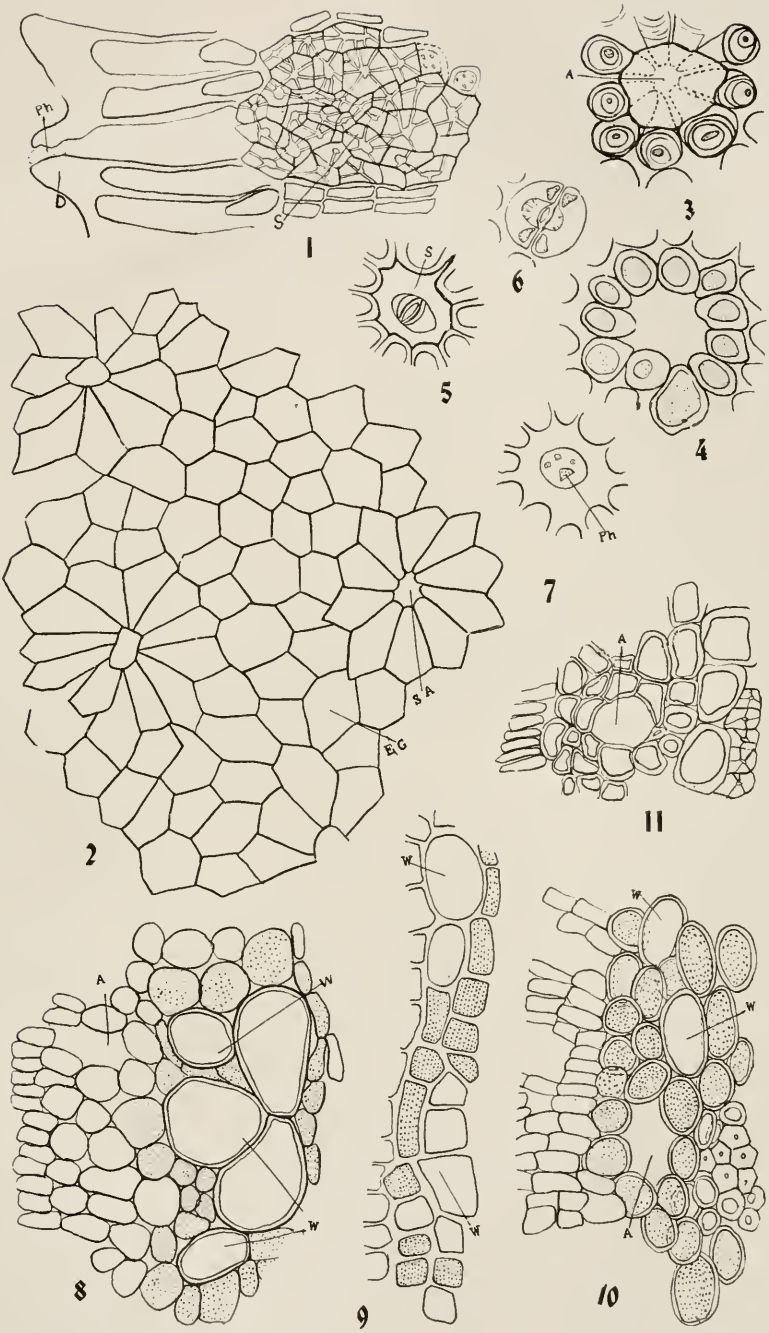
FIG. 7. Stoma proper, invaded by growth of Phycomycete, *Ph*. Tangential section.

FIG. 8. Water-storage cells, *W*, in flower branch, and aerating space, *A*. Cross, × 283.

FIG. 9. Portion of older stem, showing empty cells, *W*, probably for water storage. Cross, × 283.

FIG. 10. Water-storage cells, *W*, and aerating space, *A*, in flower branch. Cross, × 283.

FIG. 11. Aerating space, *A*, in spongy parenchyma. Longi-section, × 283.


Ph
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S
1
A
3
6
S
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Ph
7
2
S
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E
G
A
11
W
A
W
W
8
W
9
W
A
10

PLATE XXIV.

FIG. 1. Resinous-gum cells, *RD*, surrounding vascular bundles in elongated portion of receptacle. Cross, × 283.

FIG. 2. Resinous-gum cells in elongated portion of receptacle, *RD*. Longi-section, × 283.

FIG. 3. Resinous-gum cells, *RD*, surrounding ovule. × 283.

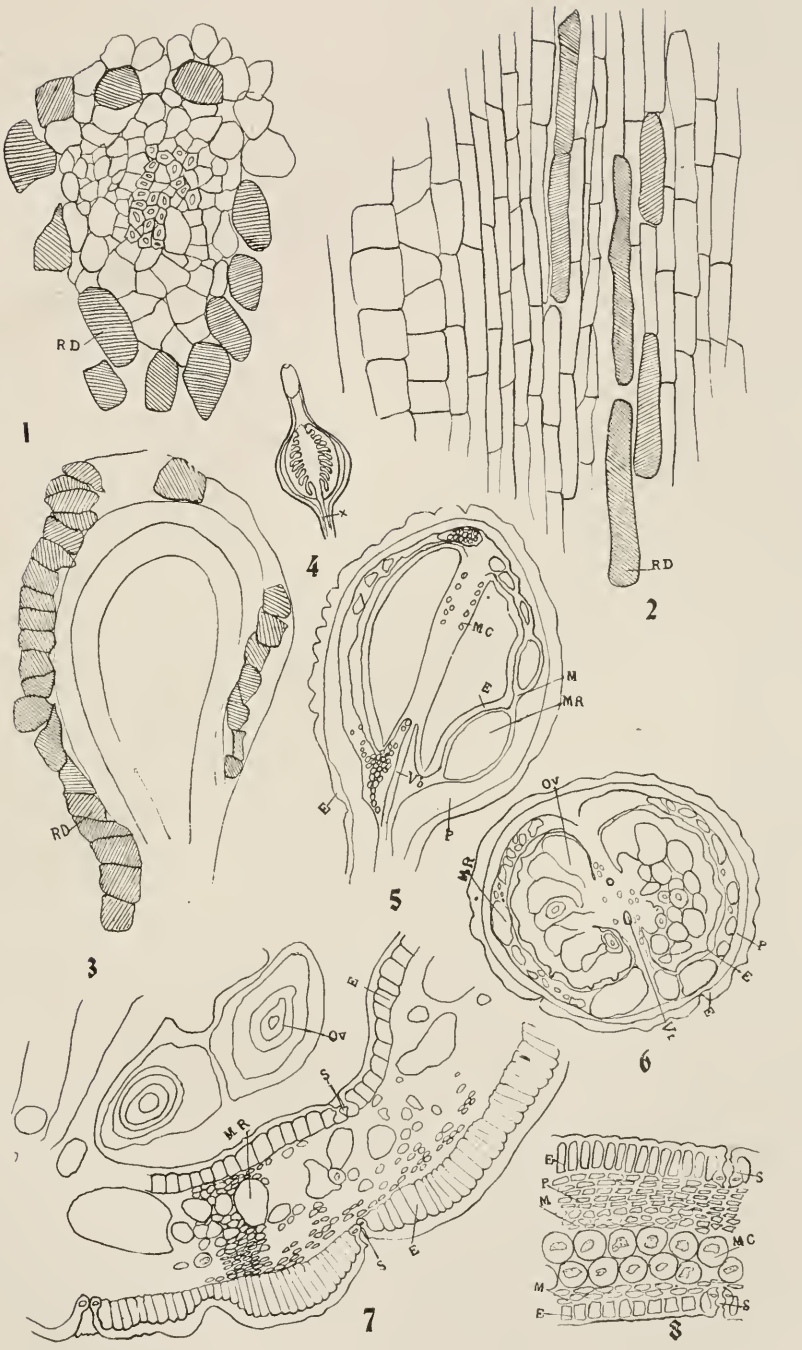
FIG. 4. Section of ovary. *X*, position of structures shown in figs. 1 and 2. Longi-section, × 5.

FIG. 5. Section showing position of mucilage reservoirs and other tissues in ovary. *MR*, mucilage reservoirs; *MC*, mucilage cells; *E*, epidermis; *p*, palisade tissue; *M*, mesophyll; *vb*, vascular bundle. Longi-section, × 55.

FIG. 6. Ovary. Reference letters same as (5). Cross, × 55.

FIG. 7. Portions of (6) more in detail. *OV*, ovule; *S*, stoma; for the other letters, see (5). Cross, × 283.

FIG. 8. Diagrammatic representation of regions in wall of ovary. Reference figures as above. Cross section enlarged.


RD
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RD
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RD
3
MC
M
MR
E
Vb
E
P
5
OV
MR
P
E
Vb
6
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OV
MR
S
E
Vb
7
E
P
M
S
MC
M
E
S
8

PLATE XXV.

FIG. 1. Portion of ovary wall in detail. *OE*, outer epidermis; *M*, mesophyll; *Mr*, mucilage reservoirs; *IE*, inner epidermis; *IS*, inner stoma; *VB*, vascular bundles. Cross, × 283.

FIG. 2. Stoma from inner epidermis of ovary wall. Cross, × 283.

FIG. 3. Outline of portion of ovary wall, showing frequency of inner stomata, *S*. Cross, enlarged.

FIG. 4. Outer stoma, enlarged. Cross, × 283.

FIG. 5. Inflorescence, showing fruit. × 1.

FIG. 6. Single flower stalk. Sepals and petals dropped. Stamen *L* longer than stamen *S*. × 5.

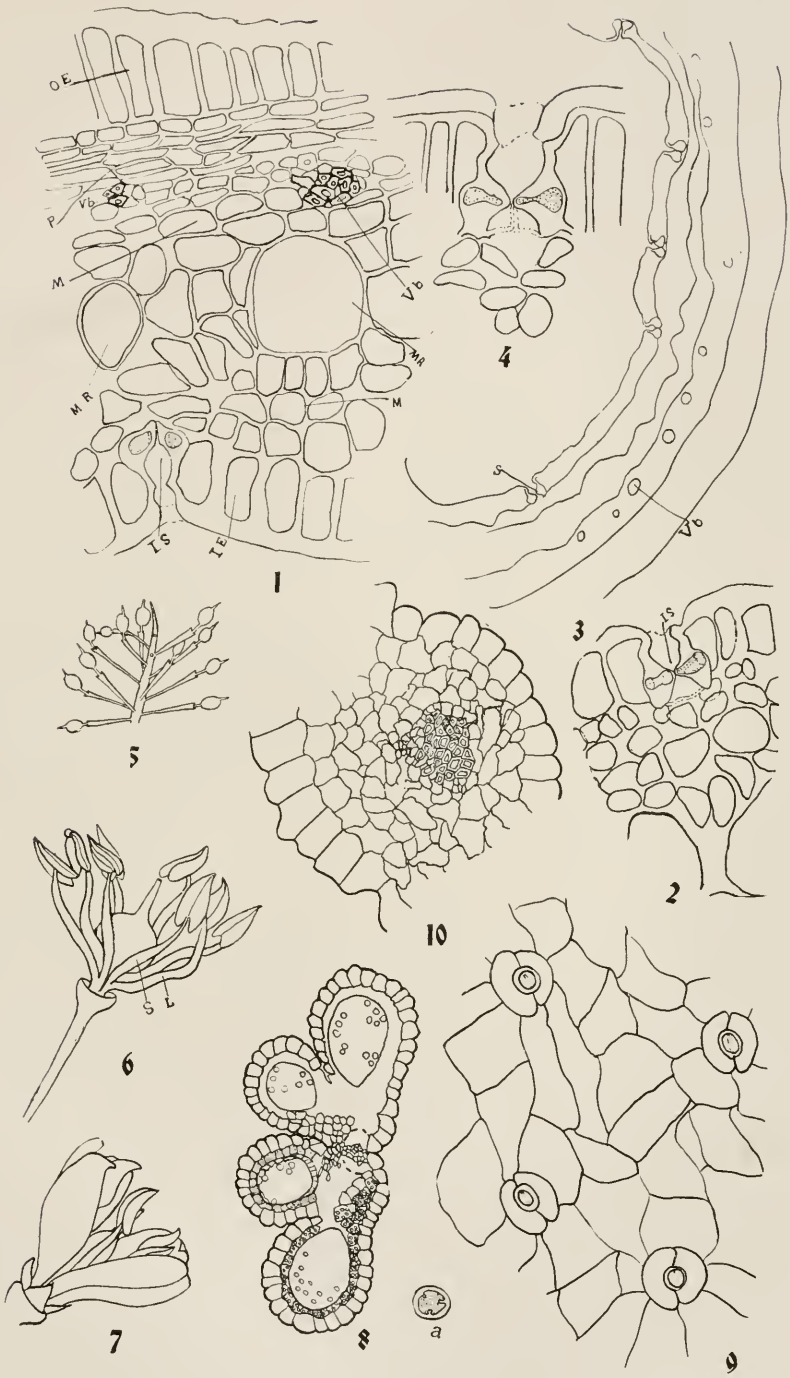
FIG. 7. Single flower. × 5.

FIG. 8. Section of anther, showing number of locules and thin-walled epidermis. Cross, × 283.

FIG. 8*a*. Pollen grain. × 636.

FIG. 9. Sunken stomata on outer epidermis of petals. × 283.

FIG. 10. Portion of petal, showing thin-walled epidermis. Cross, × 283.


OE
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SL
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PLATE XXVI.

FIG. 1.—Cross section through ovipositor, about midway: A. *cmgd*, cement gland duct; *ovid*, oviduct; *uv*, upper valve; *lv*, lower valve; *tg*, tongue and groove; *spg*, subgenital plate. B. Diagram showing position of ovipositor relative to plates.

FIG. 2.—Sport anal (?) vein of adult: *A*, anal vein; *C*, costa; *sv*, sport anal (?) vein.

FIG. 3.—Diagram of tracheation of nymphal wing pad of *P. celtidis-gemma* fore wing: *C*, costa; *Sc*, subcosta; *R*, radius; *M*, media; *Cu*, cubitus; *af*, anal fold; *A*, anal vein.

FIG. 4.—Diagram of tracheation of wing of recently emerged adult of *P. celtidis-mammæ*, fore wing.

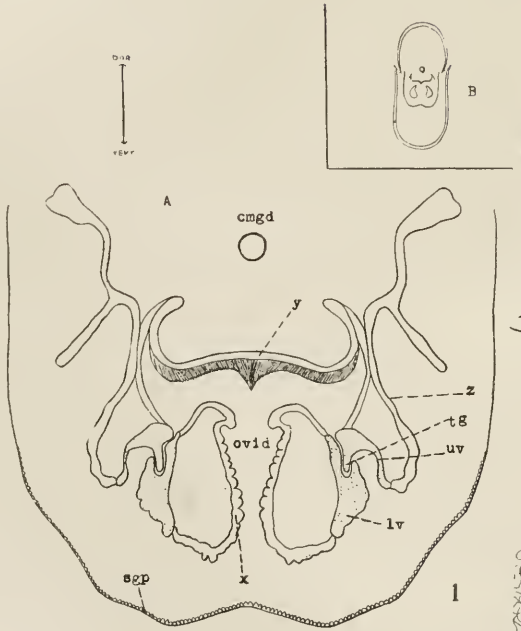
FIG. 5.—Longitudinal-vertical section through wax glands: A. *wg*, wax glands; *n*, nucleus; *cu*, cuticula; *sh*, sense organs; *wgd*, wax gland ducts; *fb*, fat body. B. *wgo*, openings of wax glands, dorsal aspect.

FIG. 6.—Tip of mandible.

FIG. 7.—Tip of maxilla.

FIG. 8.—Base of mandible: *te*, tendon.

FIG. 9.—Base of maxilla.



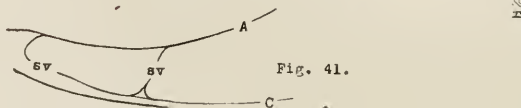


Fig. 41.

Fig. 39.

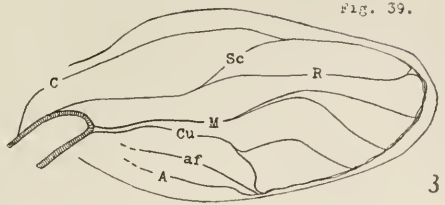
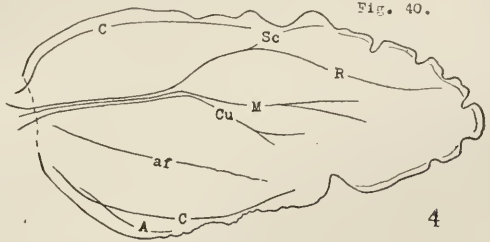


Fig. 40.



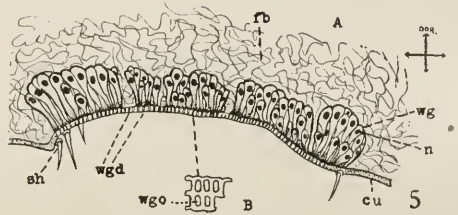


Fig. 25. ×5000.

Fig. 26. ×5000.

Fig. 27. ×6

Fig. 28. ×65

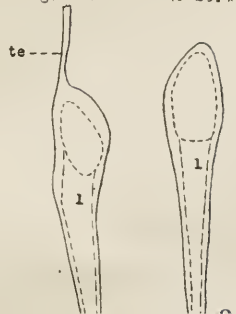


PLATE XXVII.

FIG. 1.—Lateral aspect of prothorax and mesothorax, diagrammatic: *pn*, pronotum; *es 1*, proepisternum; *es 1*, proepimeron; *pstr*, prosternum; *pcox*, procoxa; *sp*, spiracle; *dor*, dorsulum; *mm*, mesonotum; *scu*, scutellum; *artep*, articulatory epidemes; *bp*, base of primary; *em 2*, mesoepimeron; *es 2*, mesoepisternum; *mstr*, mesosternum; *end*, portion of endoskeleton.

FIG. 2.—Caudal aspect of mesothorax, diagrammatic: *ter*, tergum; *str*, mesosternum; *phr*, phragma; *apoph*, apophyse; *c*, canal; *apod*, apodeme; *es 2*, mesoepisternum; *em 2*, mesoepimeron; *end*, portion of endoskeleton corresponding to *end* in fig. 1, plate XXVII.

FIG. 3.—Sclerites forming tergum of thorax: A. *pn*, pronotum of prothorax; *dor*, dorsulum of mesothorax; *mm*, mesonotum of mesothorax; *scu*, scutellum of mesothorax; *mett*, metathorax. B. *median*, longitudinal section through tergum.

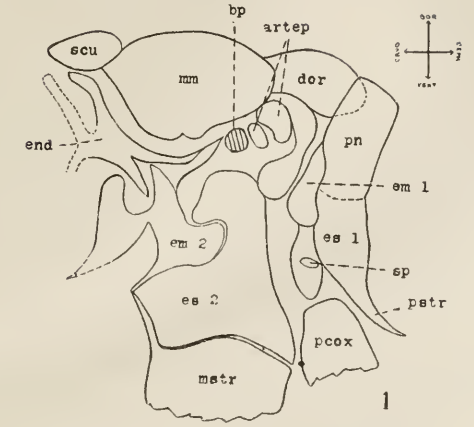
FIG. 4.—Chitinized process holding labium to thorax (cephalic aspect): A. *a*, lateral arm of process; *b*, yoke-like piece connecting lateral arms, caudad and dorsad of labium. B, tip of a lateral arm.

FIG. 5.—Ventral aspect of metathorax, diagrammatic: *str*, metasternum; *cox*, coxa; *em 3*, metaepimeron; *mer*, meracanthus; *troc*, trochanter; *mf*, ventral edge of metafurca.

FIG. 6.—Venation of adult of *P. celtidis-mammæ*, fore wing: *c*, costa; *Sc + R*, subcostal plus radius; *s*, stigma; *Sc*, subcosta; *R*, radius; *M 1 2*, media; *M 3 4*, media; *Cu 1*, cubitus; *Cu 2*, cubitus; *af*, anal fold or "claval suture"; *cl*, clavus; *A*, anal vein; *Pc*, petiolus cubite.

FIG. 7.—Venation of adult of *P. celtidis-mammæ*, hind wing.

FIG. 8.—Ventral aspect of subgenital plate of female: *b*, base of plate; *a*, apex of plate; *sh*, sensory hairs.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pn
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em 2
es 1
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es 2
pstr
pcox
mstr
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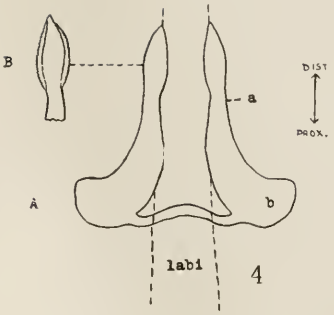
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A
b
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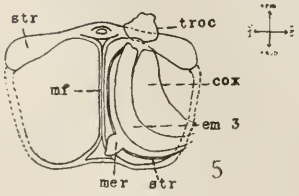
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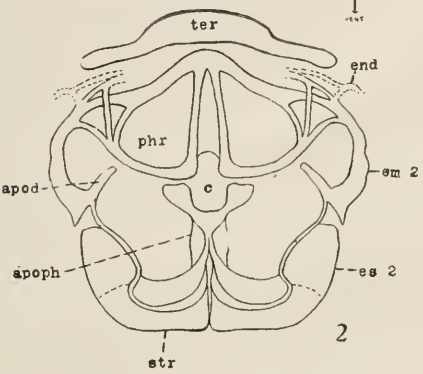
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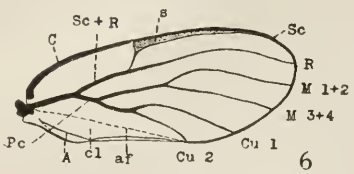
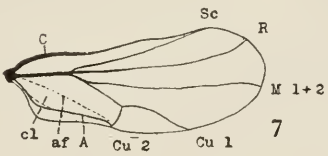

Sc + R
s
C
Sc
R
M 1+2
M 3+4
Pc
A
cl
af
Cu 2
Cu 1
6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cl
af
A
Cu 2
Cu 1
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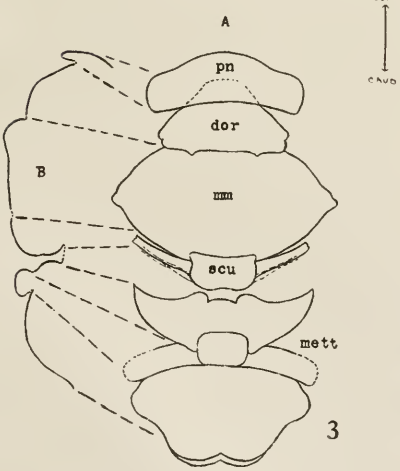
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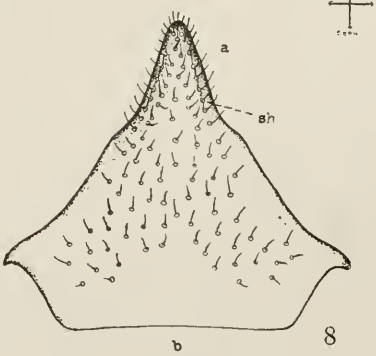
a
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8

PLATE XXVIII.

FIG. 1.—Caudal aspect of head: *ep*, epicranium; *e*, compound eye; *fo*, front ocellus; *g*, gena; *fc*, frontal cone; *a*, antennal segments; *y*, projection from gena; *x*, portion of membrane forming fold around labium between procoxæ.

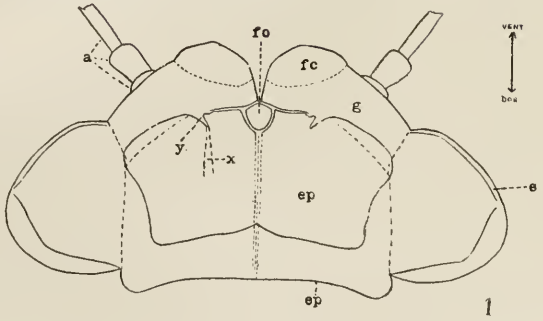
FIG. 2.—Longitudinal section of front ocellus: *cu*, cuticula; *hyp*, hypodermis; *l*, lens; *ip*, iris pigment; *v*, vitreous body; *r*, retinal cells; *n*, nerve.

FIG. 3.—Antenna.

FIG. 4.—Cephalic aspect of head: *ep*, epicranium; *e*, compound eye; *o*, ocellus; *fo*, front ocellus; *g*, gena; *fc*, frontal cone; *a*, antennal segments; *as*, antennal socket.

FIG. 5.—Ventral aspect of head: *ep*, epicranium; *e*, compound eye; *fo*, front ocellus; *g*, gena; *fc*, frontal cone; *as*, antennal socket; *p*, projection from edge of antennal socket; *y*, projection from gena; *f*, frons; *lp*, ligamentary process of frons.

FIG. 6.—Articulation between third and fourth antennal segments: *a*, third segment; *b*, fourth segment; *cor*, corrugations; *sh*, sensory hairs.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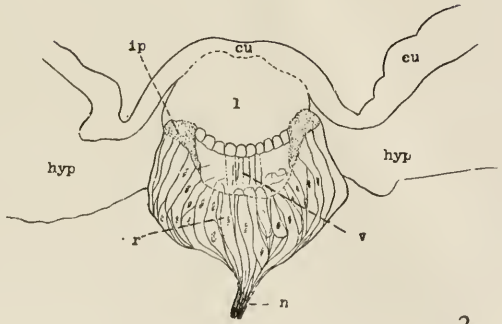
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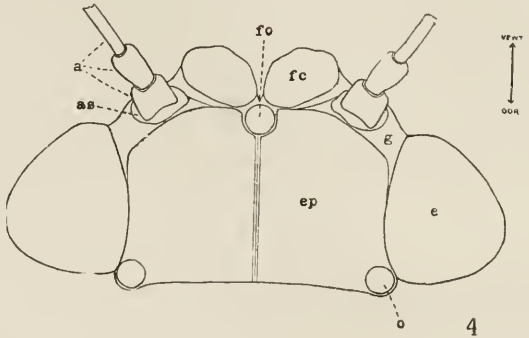
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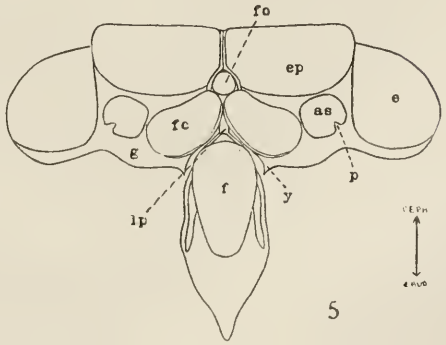
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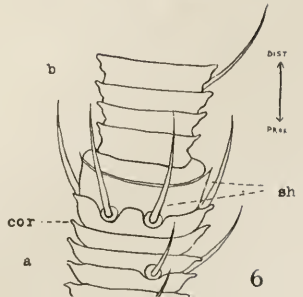
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a

6

PLATE XXIX.

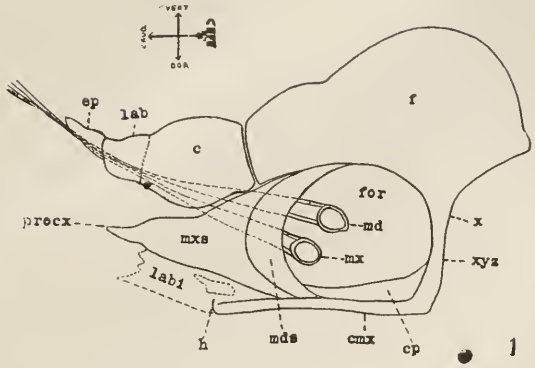
FIG. 1.—Lateral aspect of mouth parts, labium excepted: *f*, frons; *c*, clypeus; *lab*, labrum; *ep*, epipharynx; *md*, mandible; *mx*, maxilla; *mds*, mandibular sclerite; *mxs*, maxillary sclerite; *cmx*, chitinized plate for muscular attachment; *cp*, hypopharyngeal lamella; *procx*, maxillary process; *labi*, labium (base); *h*, hypopharynx; *for*, foramen.

FIG. 2.—Lateral aspect of mouth parts (diagrammatic): *f*, frons; *ep*, epipharynx; *s*, setæ; *labi 1*, *labi 2*, *labi 3*, three segments of labium; *mestr*, mesosternum; *p*, process of thorax for holding labium; *m*, membrane forming fold between procoxæ for labium.

FIG. 3.—Ventral aspect of mouth parts, labium excepted: *f*, frons, *c*, clypeus; *lab*, labrum; *ep*, epipharynx; *md*, mandible; *ms*, maxillæ; *cmx*, chitinized plate for muscular attachment; *cp*, hypopharyngeal lamella; *mds*, mandibular sclerite; *mxs*, maxillary sclerite; *procx*, maxillary process.

FIG. 4.—Ventral aspect of labium: *f*, frons; *c*, clypeus; *lab*, labrum; *ep*, epipharynx; *labi 1*, *labi 2*, *labi 3*, three segments of labium; *b*, point where bend occurs.

FIG. 5.—Dorsal aspect of mouth parts, labium excepted: *f*, frons; *lab*, labrum; *ep*, epipharynx; *md*, mandible; *mx*, maxillæ; *cmx*, chitinized plate for muscular attachment; *cp*, hypopharyngeal lamella; *procx*, maxillary process; *h*, hypopharynx; *t*, tentorium; *z*, proximal edge of frons; *p*, pharynx.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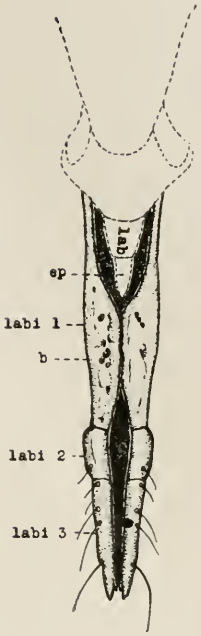
lab
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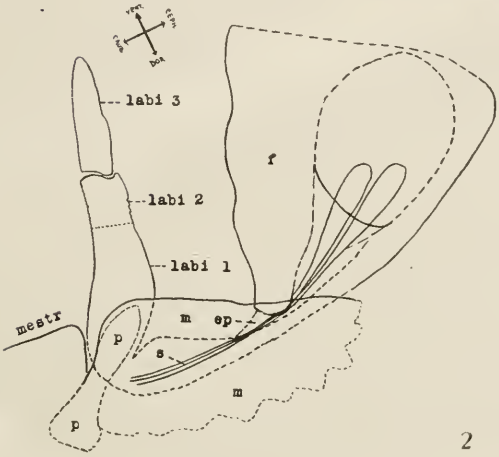
labi 1
b
labi 2
labi 3

4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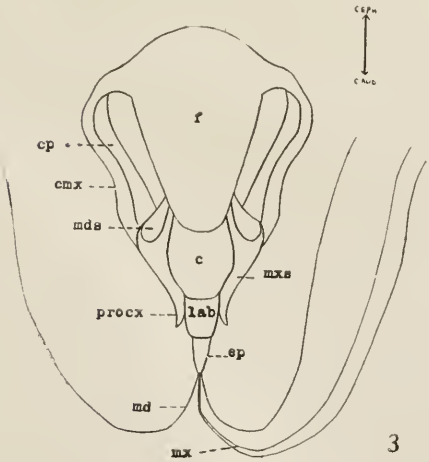
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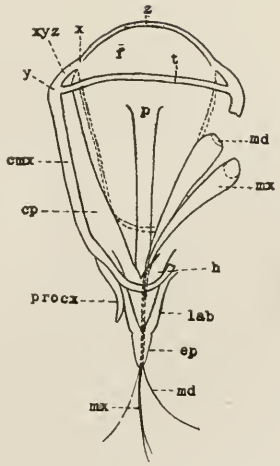
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mx

PLATE XXX.

FIGS. 1, 2 and 3.—Lateral, dorsal and ventral aspects of ovipositor, diagrammatic: *uv*, upper valves; *lv*, lower valves; *vs*, upper and lower valves (fig. 2); *buv*, base or support for *uv*; *blv*, base or support for *lv*; *sh*, sheath; *v*, valve closing oviduct; *procv*, process of rod for closing *v*; *sc*, laterally diverging pairs of sclerites cephalad of sheath (fig. 1); *sc 1*, proximal pair of sclerites; *sc 2*, distal pair of sclerites; *stp*, sting-palpi; *mr*, median rod; *lr*, lateral tendenous rod flattening out into lightly chitinized lateral plates, *lpt*.

FIG. 4.—Diagram showing position of ovipositor: *spp*, supra-anal plate; *a*, opening of anus; *sgp*, subgenital plate; *v*, valves of ovipositor; *sh*, sheath of ovipositor tip.

FIG. 5.—Lateral aspect of metafurca.

FIG. 6.—Caudal aspect of supra-anal plate: *spp*, supra-anal plate; *sppfl*, inner edges or flaps of supra-anal plate; *x*, distal portion of plate; *a*, anal opening; *lp*, lateral plate; *co*, base of copulatory organ; *l*, loop below copulatory organ.

FIG. 7.—Lateral aspect of supra-anal plate and copulatory organ: *spp*, supra-anal plate; *sppfl*, inner edges or flaps of supra-anal plate; *x*, distal portion of plate; *a*, anal opening; *lp*, lateral plate; *co*, copulatory organ; *g*, geniculation; *c*, club; *p*, penis; *l*, loop below copulatory organ; *y*, slit in base of copulatory organ.

FIG. 8.—Cephalic aspect of metathorax, diagrammatic: *str*, metasternum; *mf*, metafurca; *la*, lateral projection of endoskeleton; *mett*, metatergum.

FIG. 9.—Section through fore wing: *wm*, wing membrane; *b*, pigmented disc; *a*, unpigmented disc; *c*, cuticular processes on ventral surface of wing.

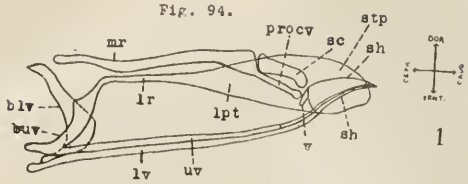
Fig. 94.
mr
procv
sc
stp
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buv
lr
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lv
uv
1

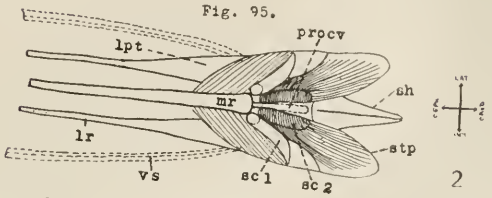
Fig. 95.
procv
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sh
mr
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sc 2
2

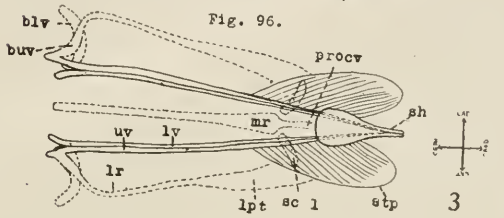
Fig. 96.
blv
buv
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sh
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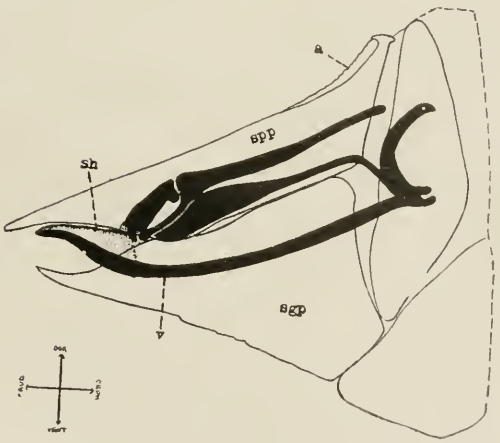
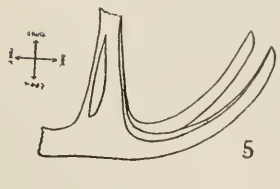
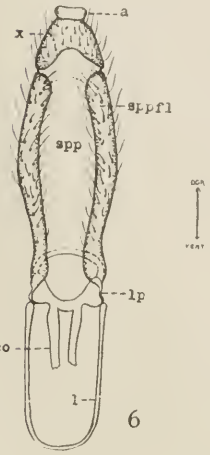
lpt
sc 1
stp
3


a
spp
sh
sgp
v
4


5

a
p
lp
c
9


a
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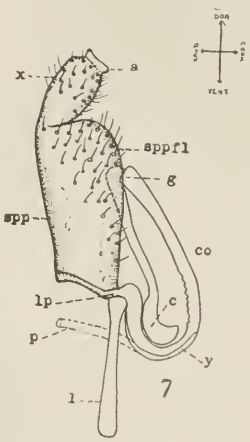
6


x
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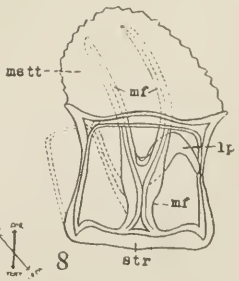
7


matt
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lp
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str
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PLATE XXXI.

FIG. 1.—Cross section through procoxæ and mouth parts: *cox*, coxa; *c*, clypeus; *p* and *pc*, parts of pharyngeal canal; *mds*, mandibular sclerite; *mxs*, maxillary sclerite; *s*, setæ; *cp*, hypopharyngeal lamella; *m*, membrane forming fold between procoxæ to hold labium.

FIG. 2.—Lateral aspect of tip of labium: *t*, lateral tongue-like processes; *sh*, sense organs.

FIG. 3.—Cephalic aspect of tip of labium: *t*, lateral tongue-like processes; *sh*, sense organs; *sl*, slit of labium.

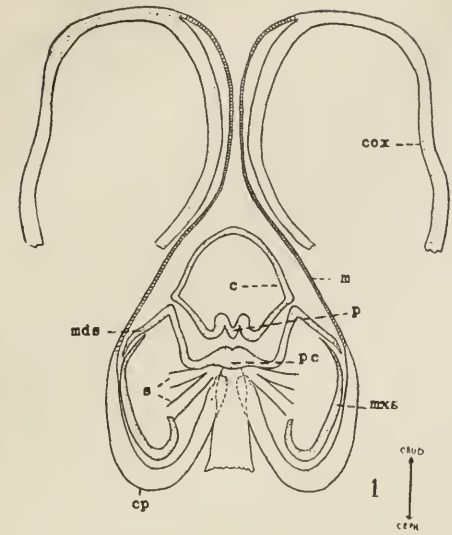
FIG. 4.—Base of supra-anal plate of female showing wax glands: *a*, anal opening; *wgo*, openings of ducts of wax glands; *sh*, sense organs; *x*, chitinized portion of plate; *y*, slightly chitinized, translucent portion of plate.

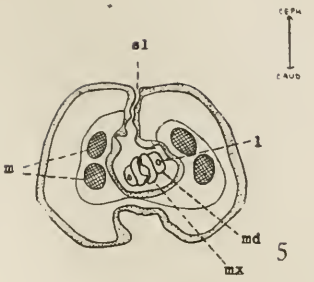
FIG. 5.—Cross section of *labi 1*: *md*, mandible; *mx*, maxilla; *m*, longitudinal muscles; *sl*, slit of labium; *l*, lumen in mandible.

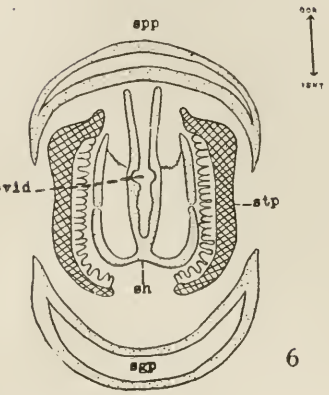
FIG. 6.—Cross section of ovipositor through base of sheath: *spp*, supra-anal plate; *sgp*, subgenital plate; *ovid*, oviduct; *sh*, sheath; *stp*, sting-palpi.

FIG. 7.—Lateral aspect of metathorax, part of metasternum, epimeron, meracanthus, coxa, etc., removed, diagrammatic: *mett*, metatergum; *mf*, metafurca; *bs*, region of base of secondary; *es 3*, region of metaepisternum; *str*, part of metasternum; *end*, a rod connected to metafurca; *x*, point of articulation of *em 3*.

FIG. 8.—Lateral aspect of metathorax, part of metasternum, episternum and metafurca removed, diagrammatic: *mett*, metatergum; *mf*, metafurca; *str*, part of metasternum; *mcr*, meracanthus; *em 3*, metepimeron; *cox*, coxa; *scl*, an accessory sclerite; *x* and *y*, articulation of *em 3*; *troc*, trochanter; *fem*, femur.







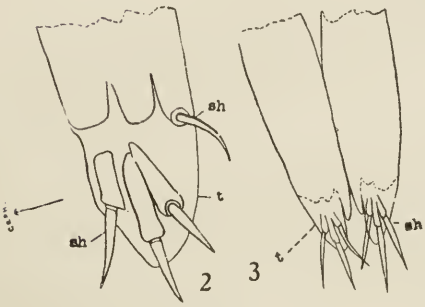
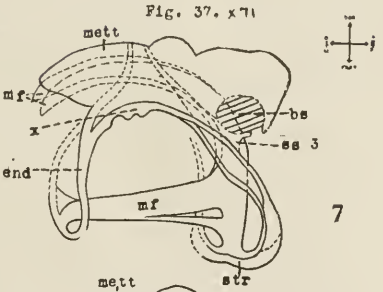
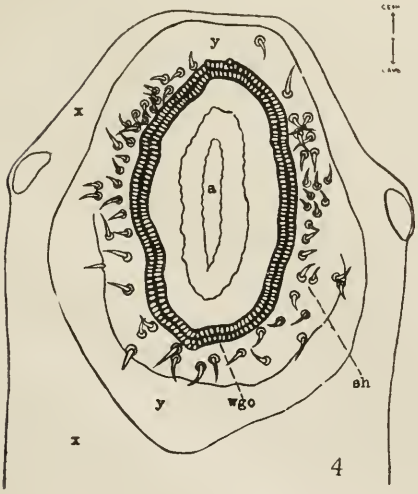


Fig. 37. x71





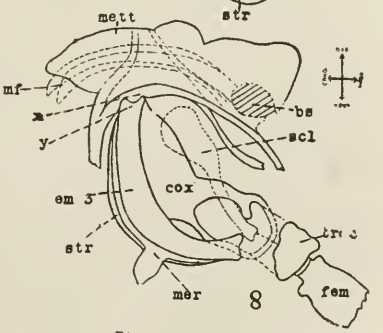


Fig. 38. x71

PLATE XXXII.

FIG. 1.—Frons and mouth parts, labium excepted, removed from head. (Photo.)

FIGS. 2, 3 and 4.—Wings of male. (Photos.)

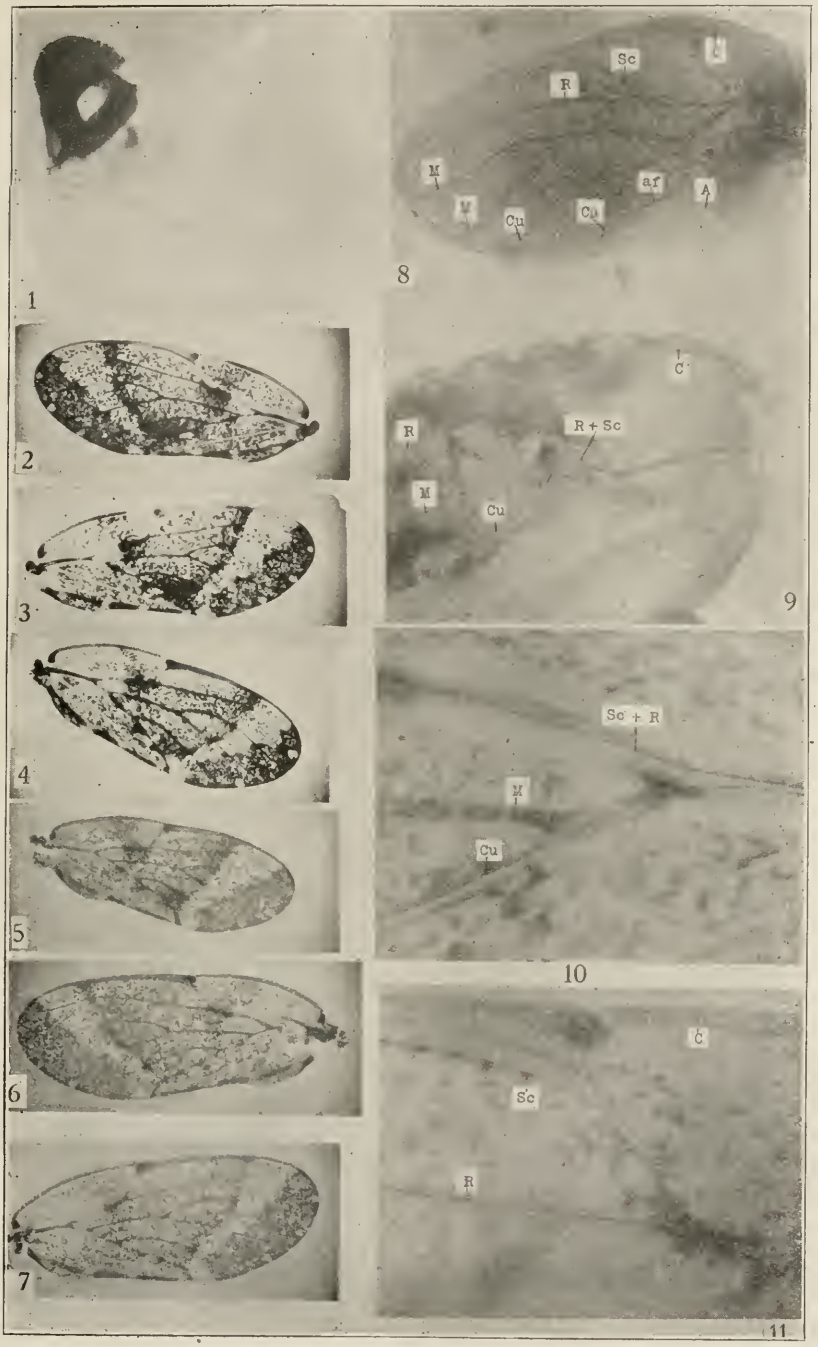
FIGS. 5, 6 and 7.—Wings of female. (Photos.)

FIG. 8.—Tracheation of nymphal wing pad of *P. celtidis-gemma*, fore wing. (Photo.) *C*, costa; *Sc*, subcosta; *R*, radius; *M*, *M*, media; *Cu*, *Cu*, cubitus.

FIG. 9.—Tracheation of wing of recently emerged adult of *P. celtidis-mammæ*, fore wing. (Photo.) *C*, costa; *Sc* + *R*, radius plus subcosta; *R*, radius; *M*, media; *Cu*, cubitus.

FIG. 10.—Branching of media and cubitus from radius plus subcosta in fore wing of recently emerged *P. celtidis-mammæ*: *Sc* + *R*, radius plus subcosta; *M*, media; *Cu*, cubitus.

FIG. 11.—Branching of subcosta and radius in fore wing of recently emerged *P. celtidis-mammæ*: *Sc*, subcosta; *R*, radius; *C*, costa.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C
R
M
M
Cu
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C
R
R + Sc
M
Cu
10
Sc + R
M
Cu
11
C
Sc
R

PLATE XXXIII.

FIG. 1.—Apex of wing of male, showing pattern. (Photo.)
FIG. 2.—Hind wing. (Photo.)
FIGS. 3 and 6.—Wings of females. (Photos.)
FIG. 4.—Highly magnified portion of pattern. (Photo.)
FIG. 5.—Apex of wing of female, showing pattern. (Photo.)
FIG. 7.—Wing of male. (Photo.)
FIG. 8.—Base of hind wing, showing pattern and hairs on costa. (Photo.)

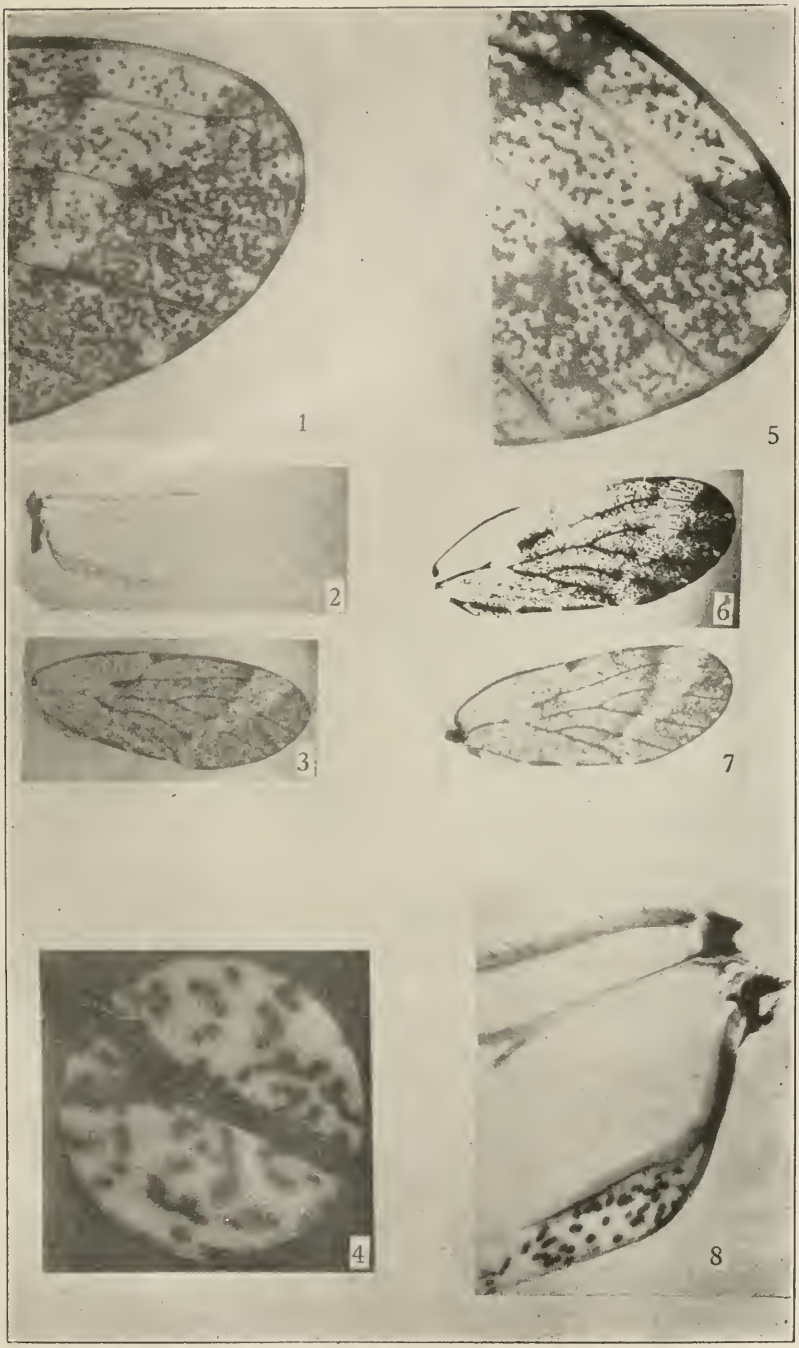
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PLATE XXXIV.

FIG. 1.— ——— Dorsal aspect of male. (Photo.)
FIG. 2.— ——— Dorsal aspect of male. (Photo.)
FIG. 3.—Ventral aspect of male. (Photo.)
FIG. 4.—Lateral aspect of female. (Photo.)
FIG. 5.—*Pachypsylla* on bark of hackberry, showing protective markings. (Photo.)
FIG. 6.—Head, antennæ, and mouth parts. (Photo.)
FIG. 7.—Photograph of head and antennæ.
FIG. 8.—Lateral aspect of mouth parts, removed from head. (Photo.)
FIG. 9.—Last four joints of antenna.

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PLATE XXXV.

FIG. 1.—Metathoracic tarsi. (Photo.)

FIG. 2.—Prothoracic tarsi. (Photo.)

FIG. 3.—Mesothoracic tarsi. (Photo.)

FIG. 4.—Dorsal aspect of supra-anal plate of female. (Photo.)

FIG. 5.—Mesothoracic leg. (Photo.)

FIG. 6.—Prothoracic leg. (Photo.)

FIG. 7.—Lateral aspect of copulatory organ. (Photo.)

FIG. 8.—Metathoracic leg. (Photo.) *scl*, accessory sclerite.

FIG. 9.—Lateral aspect of ovipositor. (Photo.)

FIG. 10.—Lateral aspect of male genitalia. (Photo.) *spp*, supra-anal plate; *sgp*, subgenital plate; *co*, copulatory organ; *f*, forceps.

FIG. 11.—Mesothoracic legs with mesosternum. (Photo.) *apoph*, apophyse.

FIG. 12.—Prothoracic legs, pronotum, etc. (Photo.) *pn*, pronotum; *es 1*, proepisternum; *em 1*, proepimeron; *cox*, coxæ.

FIG. 13.—Lateral aspect of female abdomen. (Photo.)

FIG. 14.—Lateral aspect of male abdomen. (Photo.) (Figure inverted.)

FIG. 15.—Cephalic aspect of forceps. (Photo.)

f
co
sgp
spp
10
apcph
11
ccx
en 1
es 1
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13
14
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PLATE XXXVI.

FIG. 1. Tangential section of *Populus alba* with pits in wall between medullary ray and phloëm parenchyma and between two parenchyma cells.

FIG. 2. Side view of obliquely placed end sieve plate from *Populus alba* and with pits between the sieve tubes and the other phloëm cells. Tangential section.

FIG. 3. A pit in a vertical wall between a medullary ray and the phloëm of *Populus alba*.

FIG. 4. Transverse or reticulate strengthening bands on the wall of a sieve tube in a root of *Populus deltoides*. Tangential section.

FIG. 5. Transverse bands on the wall of a sieve tube in the root of *Populus deltoides*, as seen in section.

FIG. 6. Transverse section in *Amorpha fruticosa*, showing the radially elongated medullary-ray cells and others similar to these sweeping around the narrow strip of phloëm and arranged to conduct food from these radially, especially to the cambium.

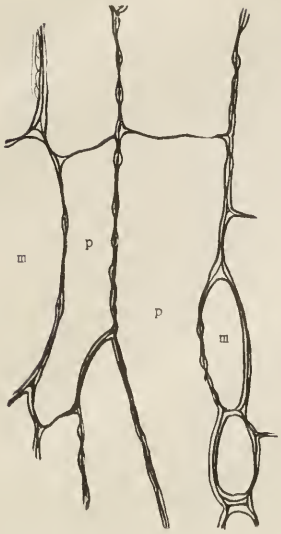
DESCRIPTION OF FIGURES.

Plates XXXVI and XXXVII.

Explanatory notes: Magnification is 600, except in figure 6, where it is 250 approximately.

Lettering: st = sieve tube; m = medullary ray; p = parenchyma; camb = cambium; stch = starch; cr = crystal; pt = pit; n = nucleus.

Symbols: $\rightarrow$) and $\rightarrow$] = direction toward nearest point of circumference or in the epidermis.



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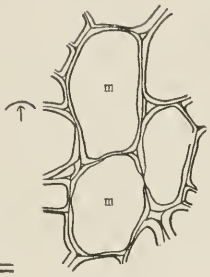

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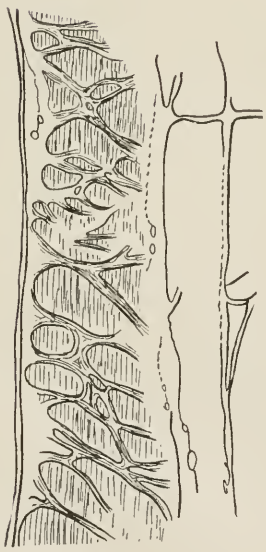

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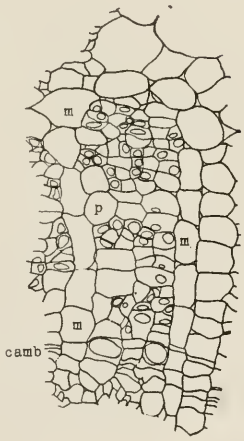


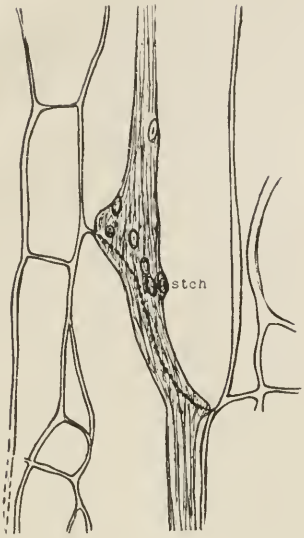
6

PLATE XXXVII.

FIG. 7. Tangential section of *Populus alba*, showing the "beaded" end plate of a sieve tube and starch granules in the slime body.

FIG. 8. Tangential section in the root of *Populus deltoides*, showing one of the remarkable obliquely placed end plates of a sieve tube in cross section. The strengthening bands here appear as larger beads and the perforation of the wall as spaces between smaller beads. This long plate evidently gives more surface for the distribution of the pits and possibly better communication between the two cells of the sieve tube.

FIGS. 9 and 10 are from tangential sections of the root of *Populus deltoides*, and show the reticulated markings caused by the pitting and banding of the obliquely placed end plates in the sieve tubes. In figure 10 the sieve tube adjoins a medullary-ray cell.



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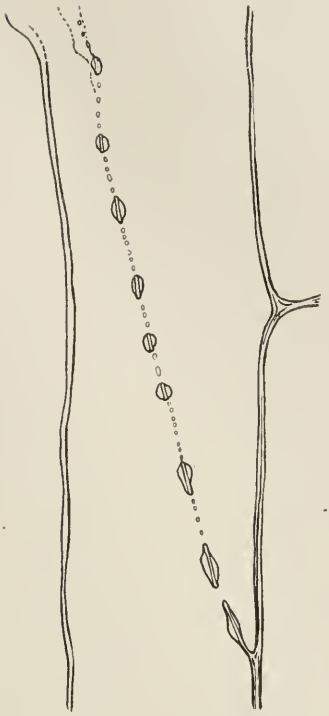

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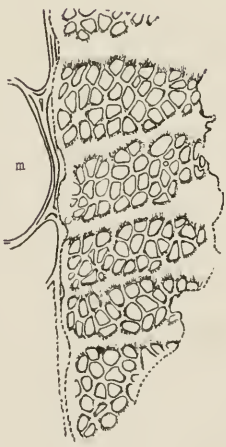


10

PLATE XXXVIII.

Townsendia exscapa.

FIG. 1. View from "Castle Rock Bluffs," Gove county, Kansas, showing the habitat of *Townsendia* in the foreground.

PLATE XXXIX.

Townsendia exscapa.

FIG. 2. Photograph of *Townsendia* in flower, showing its habit while young.

FIG. 3. Photograph of *Townsendia* in fruit, top view.

2

3

PLATE XL.

Townsendia exscapa.

FIG. 4. Cutinized epidermis of stem, cross section. *R*, outer tangential wall; *S*, inner tangential wall. × 650.

FIG. 5. Cork cells, cross section. × 650.

FIG. 6. Collenchyma cells, cross section. × 650.

FIG. 7. Collenchyma cells, longitudinal section. × 650.

FIG. 8. Short sclerenchyma cells, cross section. × 650.

FIG. 9. Short sclerenchyma cells, longitudinal section. × 650.

FIG. 10. Cortex cells, cross section. × 650.

FIG. 11. Cortex cells, longitudinal section. × 650.

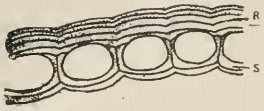
FIG. 12. Pith cells, cross section. × 650.

FIG. 13. Pith cells, longitudinal section. × 650.

FIG. 14. Small portion of xylem, cross section, showing: *a*, tracheids; *b*, wood parenchyma cells. × 650.

FIG. 15. Tracheids, as seen in a longitudinal section, when isolated from the wood parenchyma cells by means of chromic acid. × 650.

PLATE XL.



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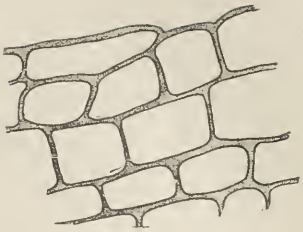

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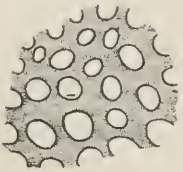

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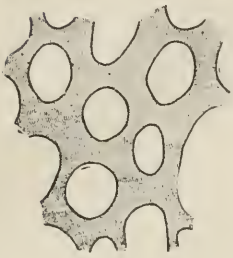

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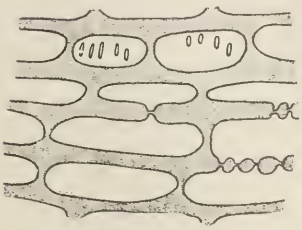

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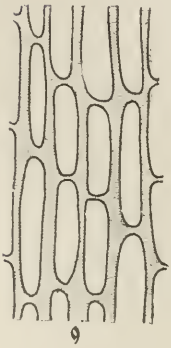

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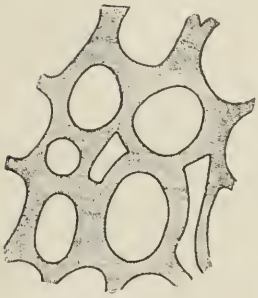

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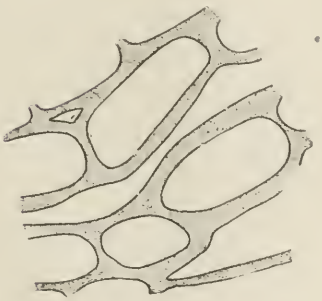

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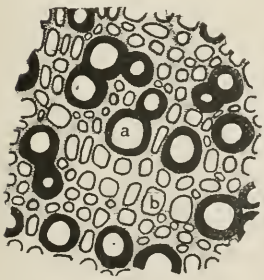

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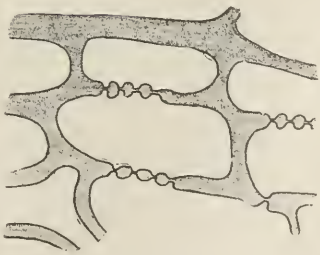

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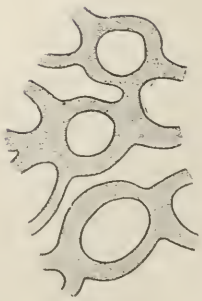


12

PLATE XLI.

Townsendia exscapa.

FIG. 16. Medullary-ray cells, cross section. × 650.

FIG. 17. Medullary-ray cells, longitudinal section. × 650.

FIG. 18. Phloëm cells, cross section. × 650.

FIG. 19. Phloëm cells, longitudinal section: *a*, cambiform cell; *b*, undivided mother cell of the sieve tubes. × 650.

FIG. 20. Cross section of root, showing the distribution of tracheids. × 115.

FIG. 21*a*. A bleached leaf, showing its method of venation. × 12½.

FIG. 21*b*. Midrib of leaf, cross section, showing: *a*, phloëm cells; *b*, tracheids; *c*, wood parenchyma cells. × 215.

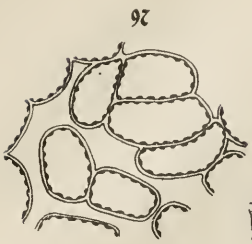
FIG. 22. Portion of a bleached leaf, showing the details of venation. × 115.

FIG. 23. Phloëm cells as seen in a longitudinal section of the midrib of a leaf: *a*, cambiform cell; *b*, undivided mother cell of the sieve tubes. × 650.

FIG. 24. Cutinized epidermis of leaf, cross section: *a*, cuticle; *b*, cutinized portion of wall. × 650.

FIG. 25. Palisade cells, surface view: *c*, intercellular spaces; *d*, palisade cell. × 650.

FIG. 26. Spongy parenchyma cells, surface view. × 650.



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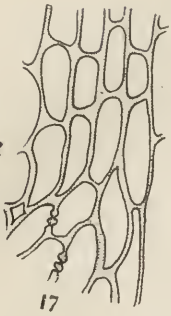

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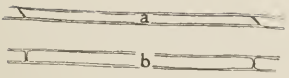

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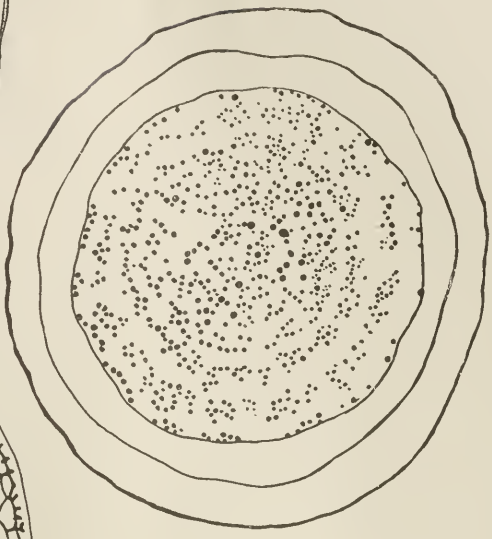

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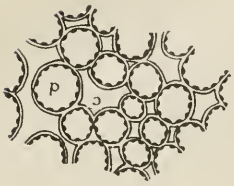

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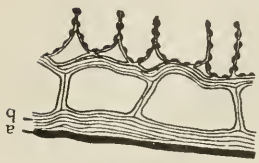

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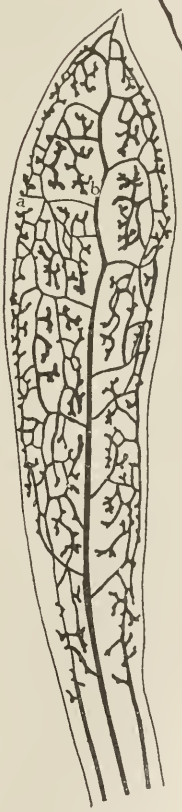
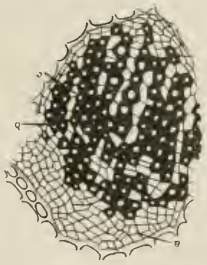


21 a



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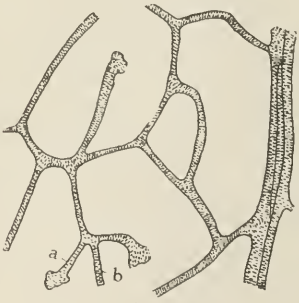

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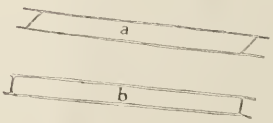

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PLATE XLII.

Townsendia exscapa.

FIG. 27. Diagrammatic drawing showing the distribution of water-storage cells as seen in cross section of a leaf: *a*, veins; *b*, water-storage cells.

FIG. 28. Palisade cells bordering on water-storage cells: *A*, water-storage cells; *B*, palisade cells; *a*, chloroplasts found in water-storage cells. × 650.

FIG. 29. Palisade cells bordering on the veins: *A*, palisade cells; *B*, border parenchyma cells; *C*, tracheids. × 650.

FIG. 30. Palisade cells bordering on water-storage cells and storage tracheids: *A*, water-storage cells; *B*, chloroplasts found in water-storage cells; *C*, water-storage tracheids; *D*, palisade cells. × 650.

FIG. 31. Palisade cells bordering on water-storage cells, which in turn border on veins: *A*, water-storage cell; *B*, chloroplasts; *C*, tracheids; *D*, border parenchyma cells. × 650.

FIG. 32. Palisade cells bordering on spongy parenchyma cells: *A*, palisade cell; *B*, spongy parenchyma cell; *C*, intercellular spaces. × 650.

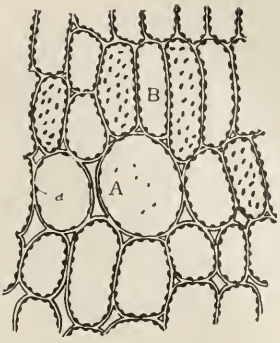
FIG. 33. Water-storage tracheids as they appear at the ultimate ends of the veins: *A*, veins; *B*, water-storage tracheids. × 650.

FIG. 34. Water-storage tracheids as they appear in other places in the leaf: *A*, ordinary tracheids; *B*, water-storage tracheids. × 650.

FIG. 35. Stomata, surface view. × 650.

FIG. 36. Stoma, as seen in cross section of the leaf. × 650.

27



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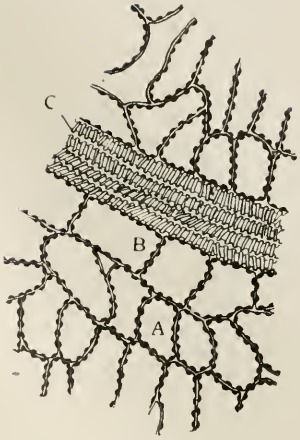

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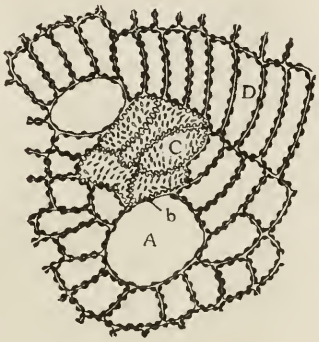

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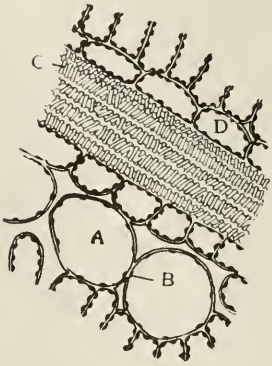

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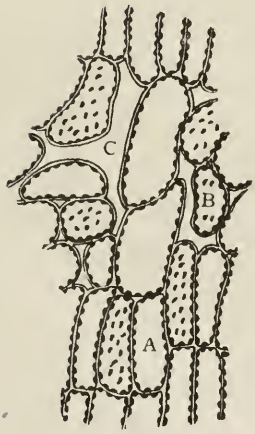

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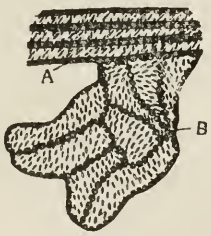

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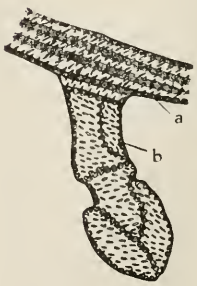

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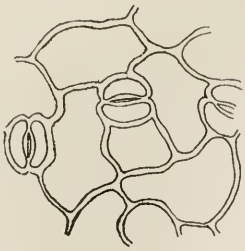

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PLATE XLIII.

Lesquerella spathulata.

FIG. 37. Cutinized epidermis of stem, cross section: *S*, outer tangential wall; *T*, inner tangential wall. × 650.

FIG. 38*a*. Cutinized epidermis of stem, longitudinal section: *S*, outer tangential wall; *T*, inner tangential wall. × 650.

FIG. 38*b*. Cork cells as seen in cross section. × 650.

FIG. 39. Stone cells found in the borke, cross section. × 650.

FIG. 40. Collenchyma cells, cross section. × 650.

FIG. 41. Collenchyma cells, longitudinal section. × 650.

FIG. 42. Stone cells found in sclerenchyma tissue, cross section. × 650.

FIG. 43. Stone cells found in sclerenchyma tissue, longitudinal section. × 650.

FIG. 44. Bast fibers, longitudinal section. × 650.

FIG. 45. Bast fibers, cross section. × 650.

FIG. 46. Small portion of xylem, cross section: *A*, wood fibers; *B*, wood parenchyma cells; *C*, tracheal elements.

FIG. 47. Wood fiber, longitudinal section. × 650.

FIG. 48. Tracheal elements found in the stem at the nodes as seen in longitudinal section: *A*, scalariform type of tracheids; *B*, spiral type of tracheids. × 650.

FIG. 49. Tracheal elements found in the internodes of the stem, as seen in longitudinal section: *A*, spiral tracheal tubes found among the wood fibers; *B*, spiral tracheal tubes found among the wood parenchyma cells; *C*, scalariform tracheal tubes. × 650.

FIG. 50. Diagrammatic drawing of the cross section of the stem: *A*, borke; *B*, collenchyma; *C*, sclerenchyma; *D*, phloëm; *E*, xylem; 1, tracheal tissues; 2, wood fibers; 3, xylem parenchyma; *F*, medullary ray; *a*, leaf trace. × 87½.

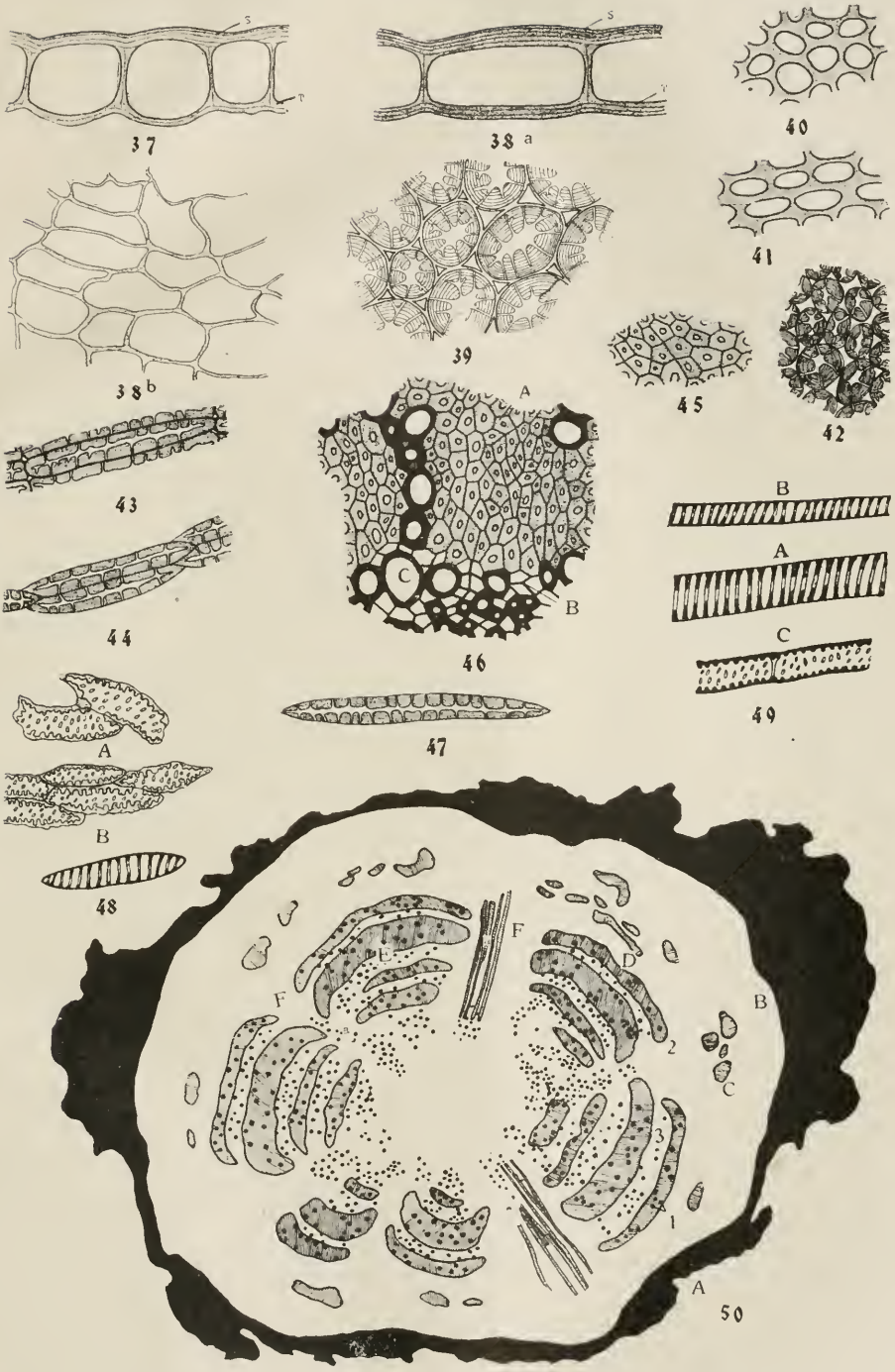

37
38 a
38 b
39
40
41
42
43
44
45
46
47
48
49
50
A
B
C
D
E
F
1
2
3

PLATE XLIV.

Lesquerella spathulata.

FIG. 51*a*. Spiral tracheal tubes found in the leaf trace. × 650.

FIG. 51*b*. Small portion of the medullary ray, as seen in cross section. × 650.

FIG. 51*c*. Phloëm cells, as seen in cross section: *A*, intercellular spaces. × 650.

FIG. 52. Phloëm cells, as seen in longitudinal section: *A*, intercellular spaces. × 650.

FIG. 53. Thin-walled parenchyma cells of the cortex, cross section. × 650.

FIG. 54. Xylem parenchyma cells, as seen in longitudinal section. × 650.

FIG. 55. Wood fibers and tracheal tubes found in the outermost layer of xylem, cross section. × 650.

FIG. 56*a*. Segment of the cross section of the root, showing the constitution of the xylem: *A*, wood fibers; *B*, tracheal elements; *C*, wood parenchyma. × 53.

FIG. 56*b*. Tracheal elements found in the root: *A* and *B*, scalariform tracheal tubes; *C*, spiral tracheal tube. × 650.

FIG. 57. Tracheal tubes and wood parenchyma cells found in the layer of xylem (fig. 56*a*, *F*): *A*, tracheal tubes; *B*, wood parenchyma cells. × 650.

FIG. 58. Wood parenchyma cells, as seen in longitudinal section. × 650.

FIG. 59. Wood fibers and tracheal tubes found in the layer of xylem (fig. 56*a*, *G*). × 650.

FIG. 60. Diagrammatic drawing of the cross section of the root, showing: *A*, cork; *B*, collenchyma; *C*, stone cells; *D*, thin-walled parenchyma; *E*, phloëm; *F*, wood fibers; *G*, wood parenchyma; *H*, tracheal elements; *I*, medullary ray. × 65.

FIG. 61. Cutinized epidermis of leaf: *A*, outer tangential wall; *a*, cutinized portion; *b*, cellulose portion; *B*, inner tangential wall. × 650.

FIG. 62. A bleached leaf, showing the method of venation: *A*, central vein; *B*, lateral branches sent off from the midrib near the center; *C*, two prominent longitudinal veins found on either side of the midrib; *D*, *E*, *F*, terminations of veins; *G*, a large lateral vein sent out from below the center of the midrib, × 27.

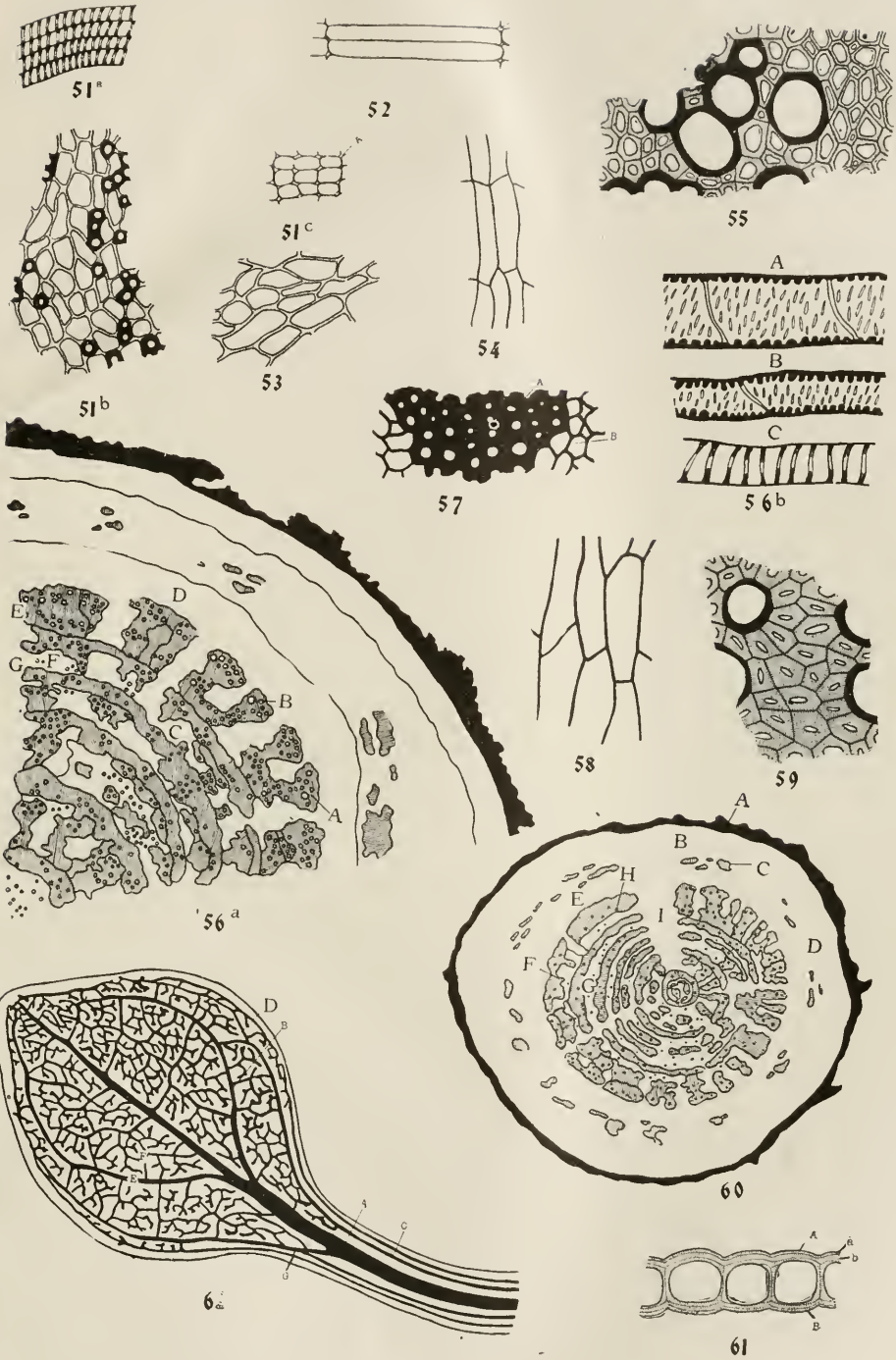

51a
52
55
51c
54
A
B
C
51b
53
57
56b
58
59
D
E
F
G
B
C
A
56a
A
B
C
H
E
I
D
F
G
60
D
B
A
C
6a
61

PLATE XLV.

Lesquerella spathulata.

FIG. 63. Small portion of midrib of leaf, as seen in longitudinal section: *A*, spiral tracheary tracheid; *B*, undivided mother cell of the sieve tubes. × 650.

FIG. 64. Palisade cells, surface view. × 650.

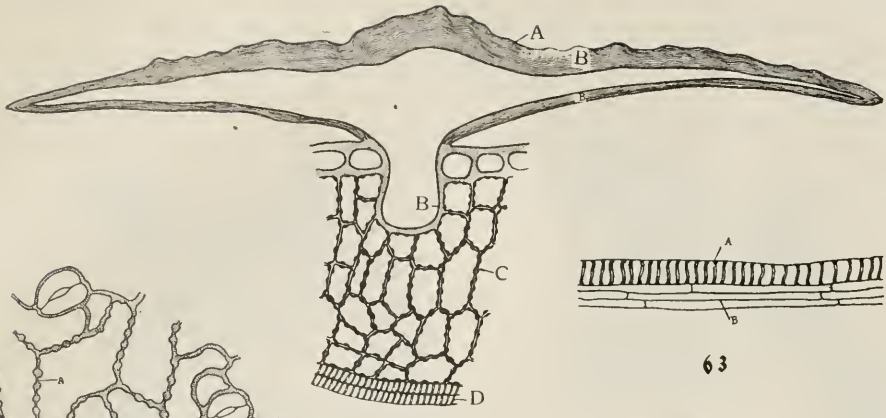
FIG. 65. Trichomes, as seen in surface view of the leaf. × 115.

FIG. 66. Trichome, as seen in leaf, cross section: *A*, cutinized portion of wall of trichome; *B*, cellulose portion of wall of trichome; *C*, mesophyll cells; *D*, tracheids. × 250.

FIG. 67. Stomata, as seen in surface view. × 650.

FIG. 68. Stoma, as seen in cross section. × 650.

FIG. 69. Leaf, as seen in cross section: *A*, upper epidermis; *B*, lower epidermis; *C*, palisade tissue; *D*, vascular bundle. × 250.



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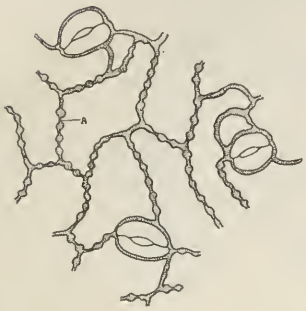

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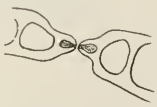

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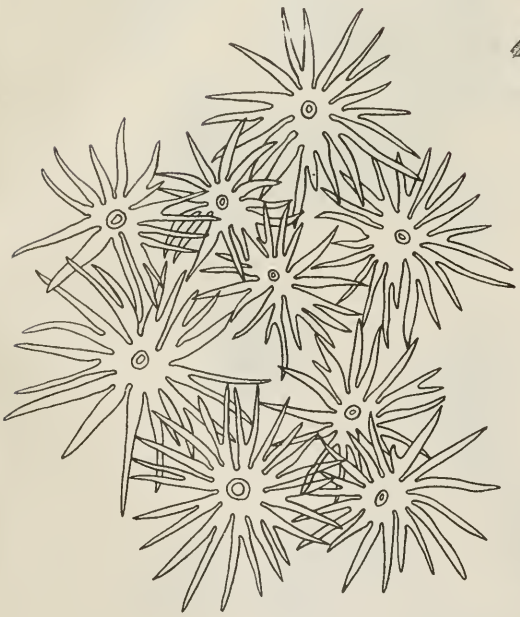

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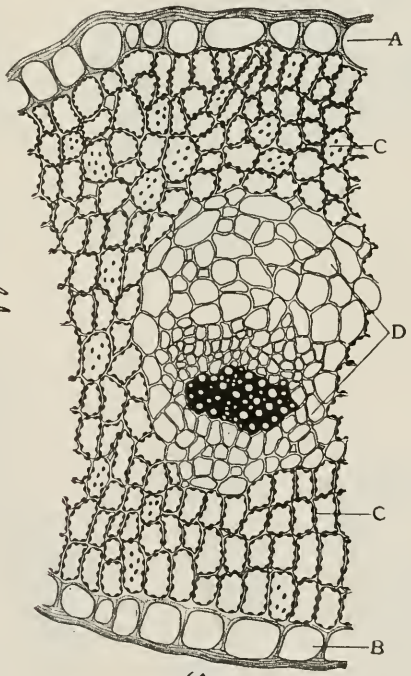

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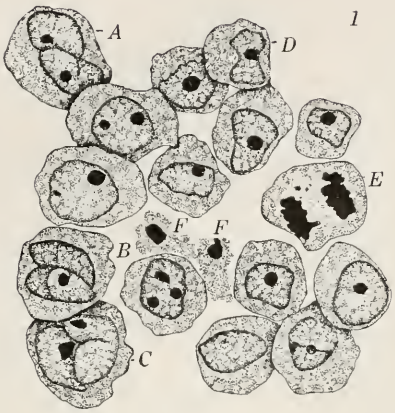
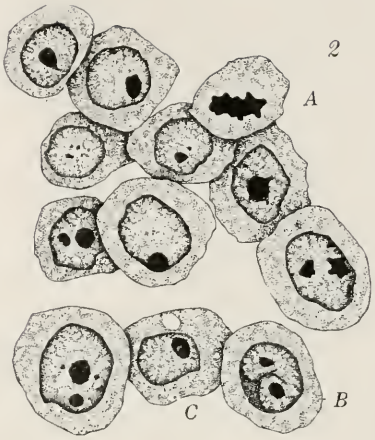
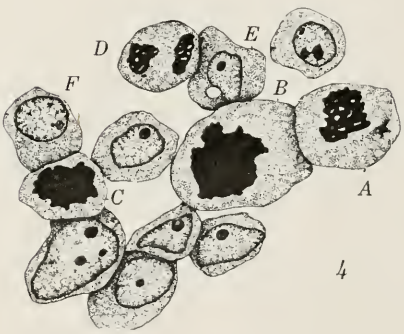
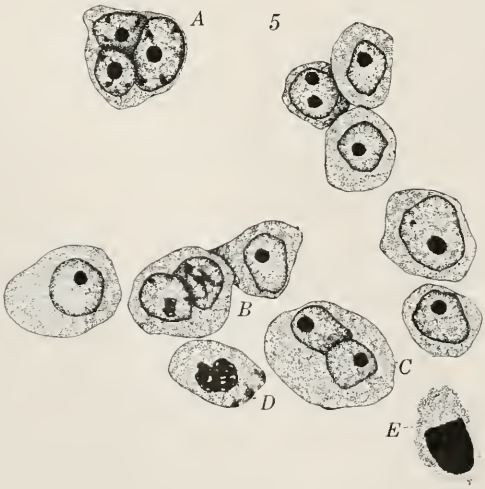
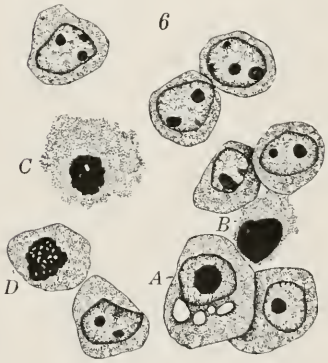

1
A
D
E
F
F
B
C

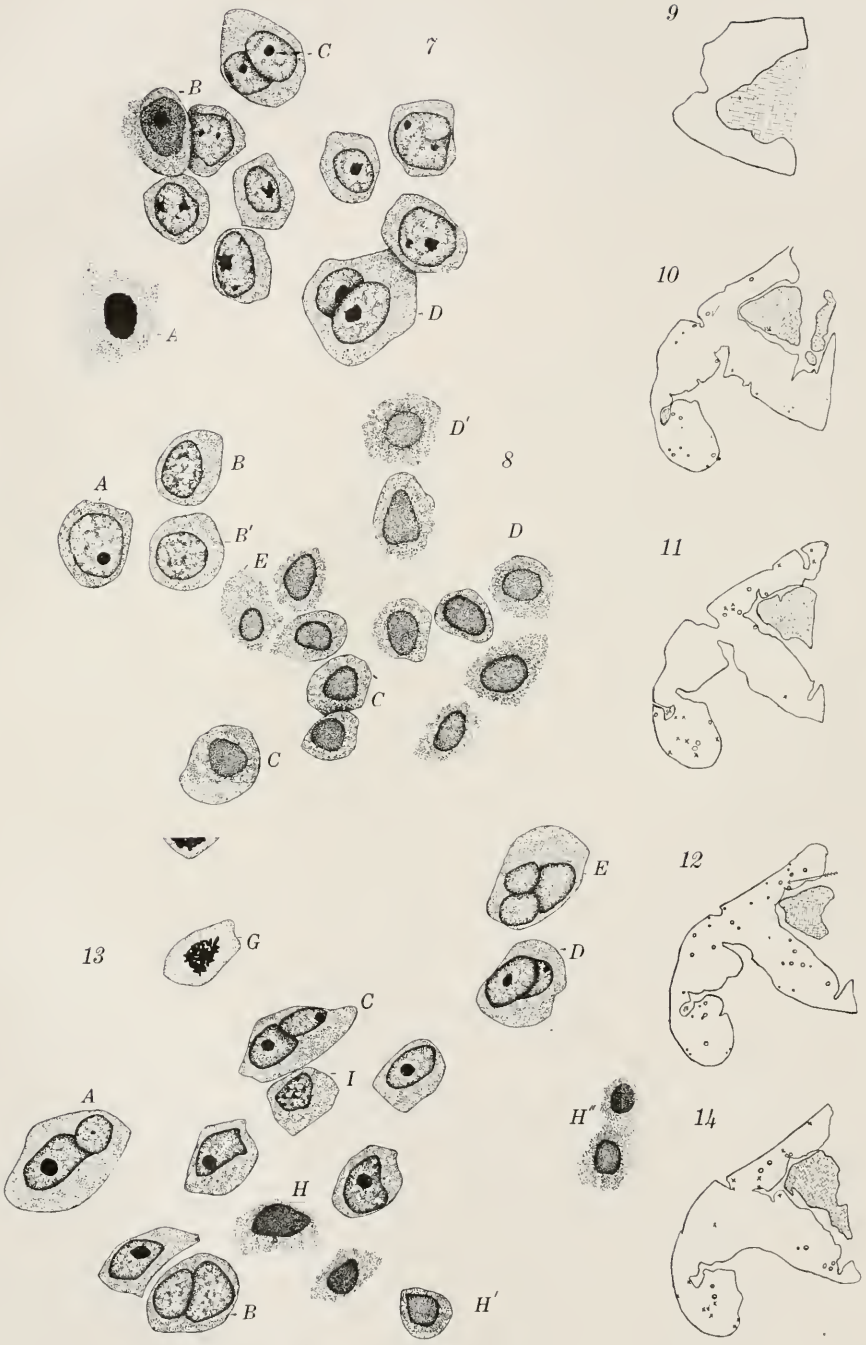

2
A
C
B

3
A
B


D
E
F
B
C
A
4


A
5
B
C
D
E


6
C
B
D
A


7
C
B
A
D
8
D′
B
A
B′
E
D
C
C
9
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11
12
13
G
E
D
C
I
A
H″
14
H
B
H′

15

16

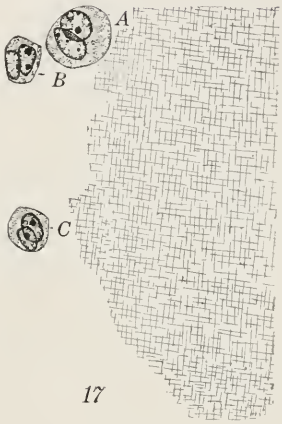

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PLATE XLIX.

FIG. 1. External view of the right mandible of *Eryops willistoni*. × ½. Drawing by S. Prentice. *a* = articular; *c* = coronoid.

FIG. 2. Maxillary tooth of *Eryops willistoni*. × ½.

FIG. 3. Fragment of cranium, including portion of right orbit and showing very distinctly the suture bounding the anterior border of the right frontal. A portion of the supraorbital lateral line canal may be also detected. × ½. O = orbit.

FIG. 4. Cross section of mandibular tooth, showing pulp cavity and dental tubules. × 2.

FIG. 5. External view of anterior portion of the right mandible. × ½.

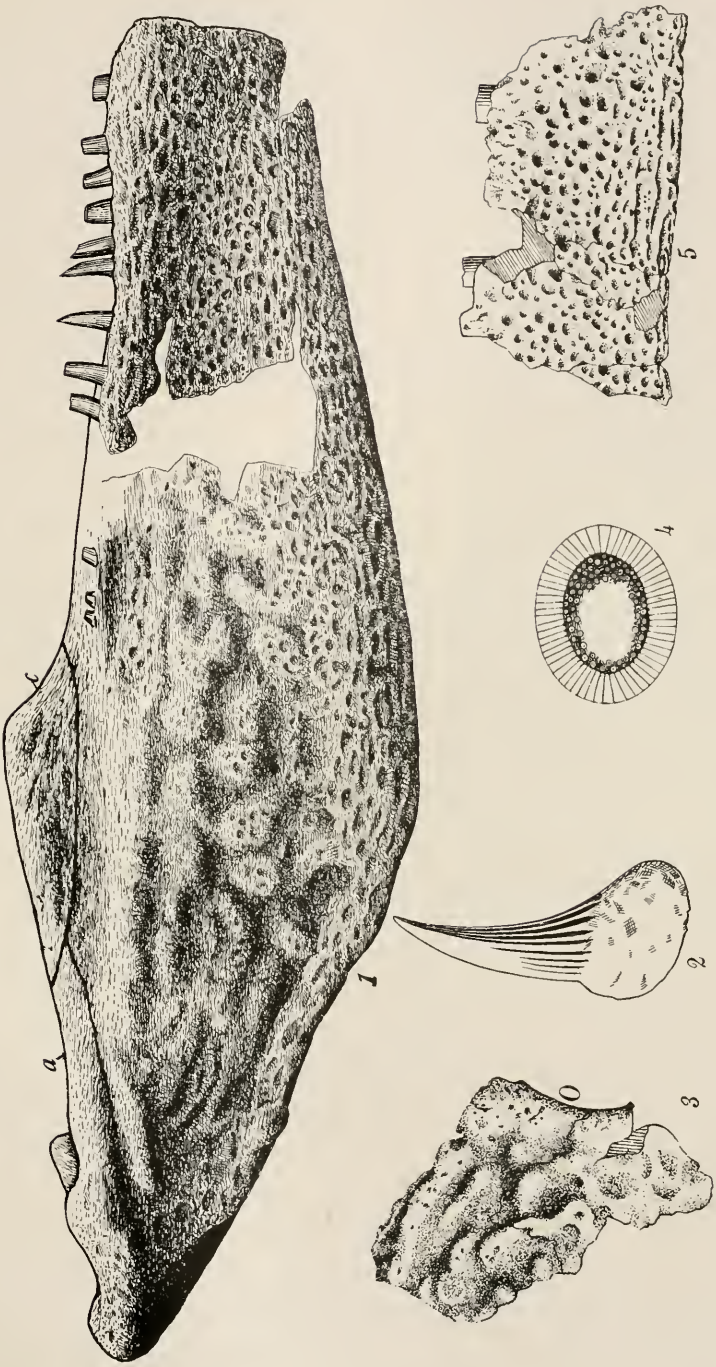
1
2
3
4
5
a
c
o

PLATE L.

External view of the right coraco-scapula of *Eryops willistoni*. × ½.
C = coracoid portion of the coraco-scapula; *f* = foramen for artery;
L = cleithrum; *O* = humeral cotylus.

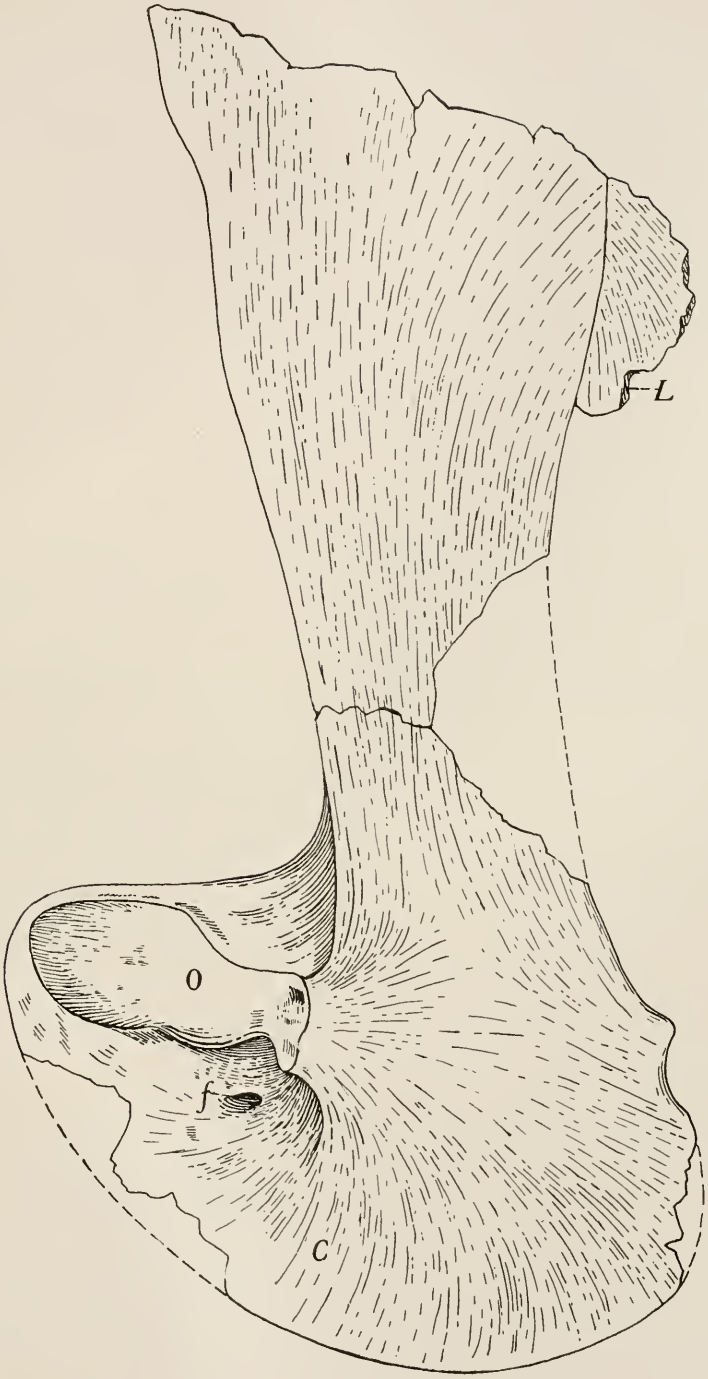
L
O
f
C

PLATE LI.

Internal view of coraco-scapula. C = coracoid portion; f = foramen; L = cleithrum. × ½.

L
f
C

PLATE LII.

Arm bones of *Eryops willistoni*. × ⅔. *H* = humerus; *R* = radius; *U* = ulna. Cross sections of the various elements are shown at the sides.

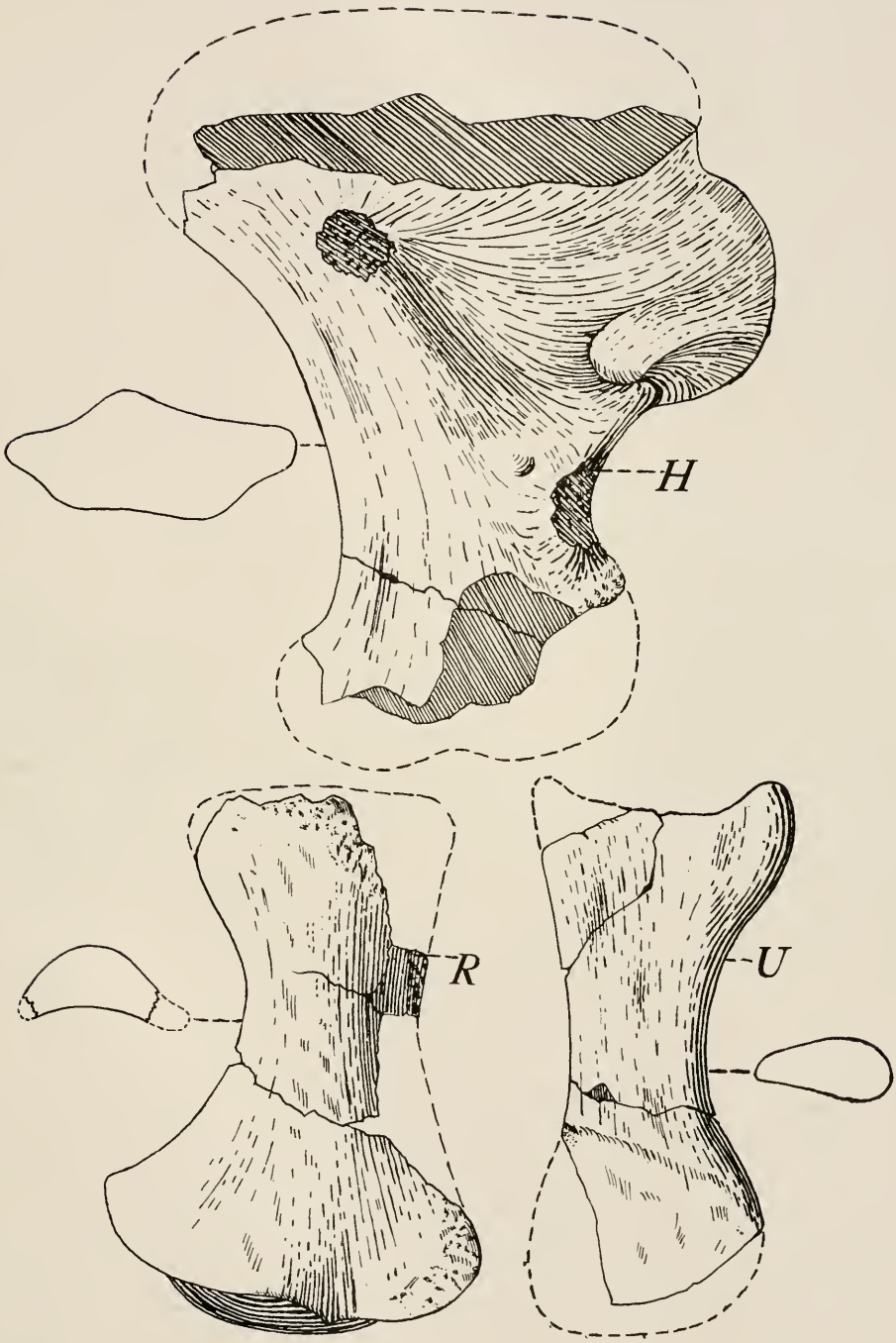
H
R
U

PLATE LIII.

FIG. 1. Posterior view of right clavicle of *Eryops willistoni*. × ⅔.

FIG. 2. Ventral view of right clavicle. × ⅔.

FIG. 3. Ventral view of the posterior projection of the interclavicle of *Eryops willistoni*. × ⅔.

FIG. 4. Dorsal view of phalange (metacarpal ?). × ⅔.

FIG. 5. End view of same. × ⅔.

FIG. 6. Cross section of posterior projection of interclavicle.

FIG. 7. Anterior view of the right humerus. × ⅔. *f* = supracondylar arterial foramen.

FIG. 8. Cross section of the clavicle.

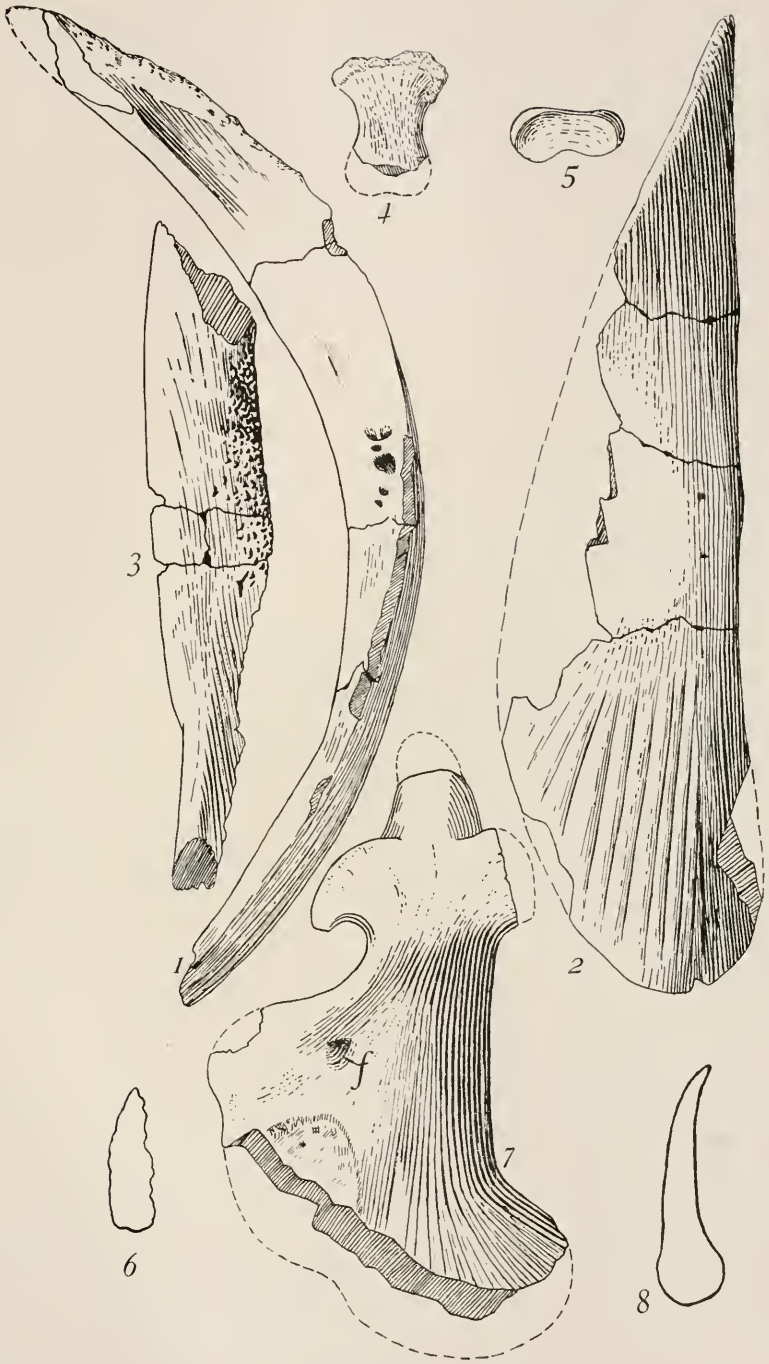
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PLATE LIV.

FIG. 1. Posterior view of a dorsal vertebral spine, showing apical enlargement. × ⅔.

FIG. 2. Lateral view of three consecutive dorsal vertebræ. × ⅔.

FIG. 3. Ventral view of left sacral rib. × ⅔.

FIG. 4. Dorsal view of the same.

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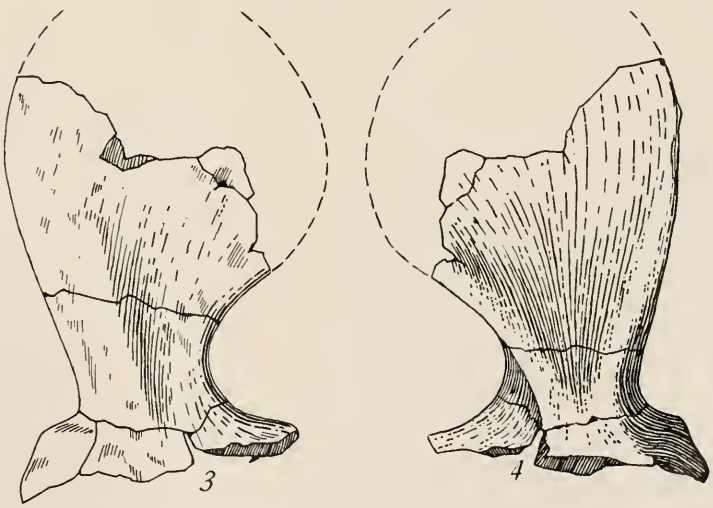
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PLATE LV.

The dorsal surface of the left ilium of *Stegopelta*, showing the dermal plates. × ¼.

PLATE LVI.

FIG. 1. A large dermal spine which was possibly associated with the heavy bony girdles near the base of the tail. × ¼.

FIG. 2. One of the massive dermal plates of *Stegopelta*, which may have formed part of another girdle like the elements in figs. 6 and 7. × ½.

FIG. 3. The median dorsal scute between the ilia. × ¼.

FIGS. 4 and 5. The teeth of *Stegopelta*. × 1½.

FIGS. 6 and 7. Dorsal and posterior views of large bony girdle, which probably encircled the tail near the base. × ¼.

FIG. 8. Detail of the surface of the left ilium; one of the dermal scutes, one-half natural size.

FIG. 9. A heavy dermal plate, which may possibly have been associated with the element shown in figure 2 to form another girdle. (See Wieland, 1909, Amer. Jour. Sci., March, p. 251, fig. 6.) × ¼.

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3
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PLATE LVII.

Dorsal view of thirteen small dermal plates of *Stegopelta*, nearly natural size, showing the various shapes, sizes, and manner of ornamentation

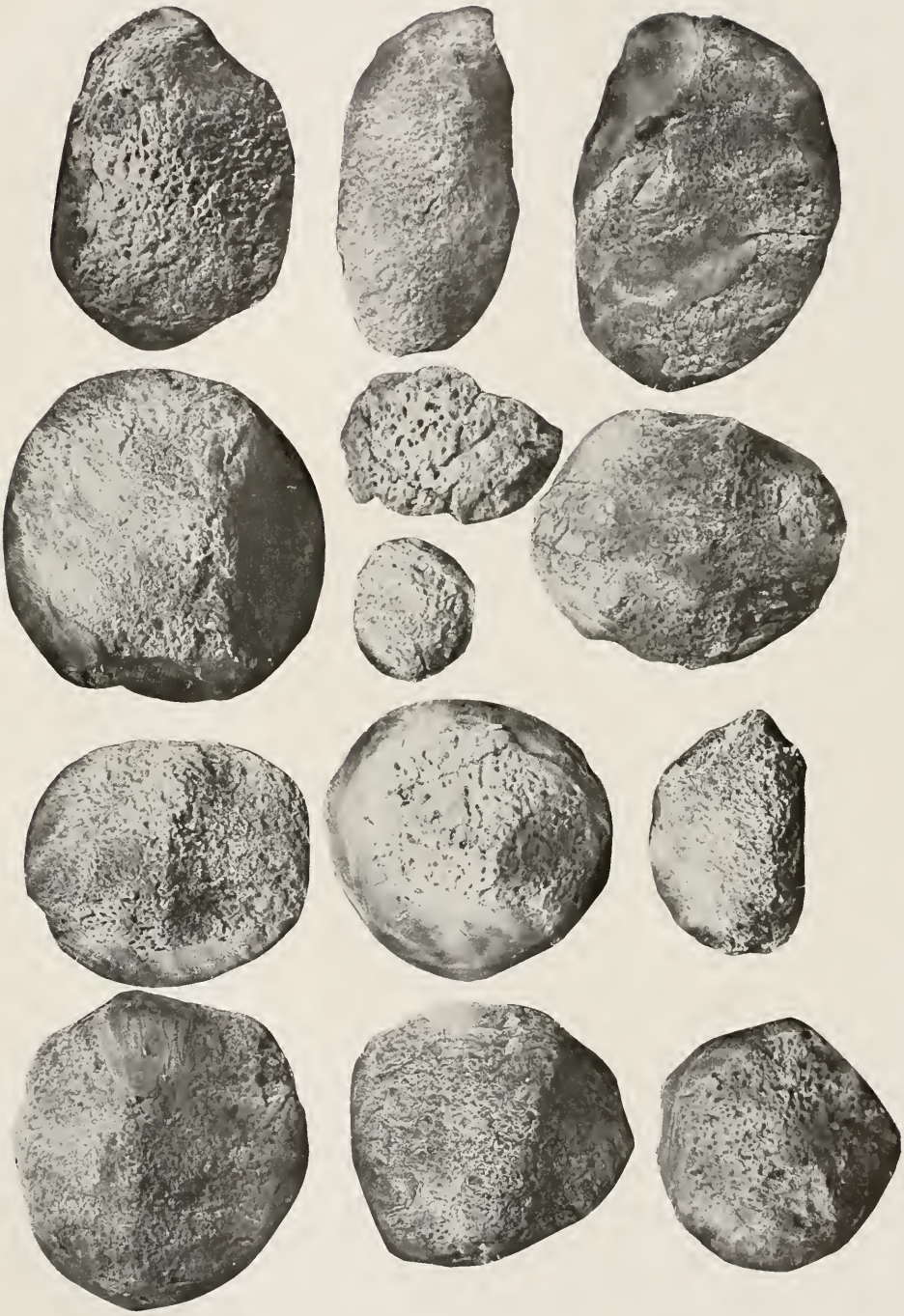

PLATE LVIII.

FIG. 1. The external surface of the right pubis. × ¼.

FIG. 2. The right pubis seen from the edge. × ¼.

FIG. 3. The posterior view of an anterior caudal or a posterior sacral vertebra. × ¼.

FIG. 4. The lower portion of the right tibia, showing the firm union of the astragalus. One-half natural size.

FIG. 5. Lateral view of one of the dorsal vertebræ. One-half natural size.

FIG. 6. Posterior surface of a dorsal vertebra. × ½.

FIG. 7. A metatarsal of *Stegopelta* seen from above. × ½.

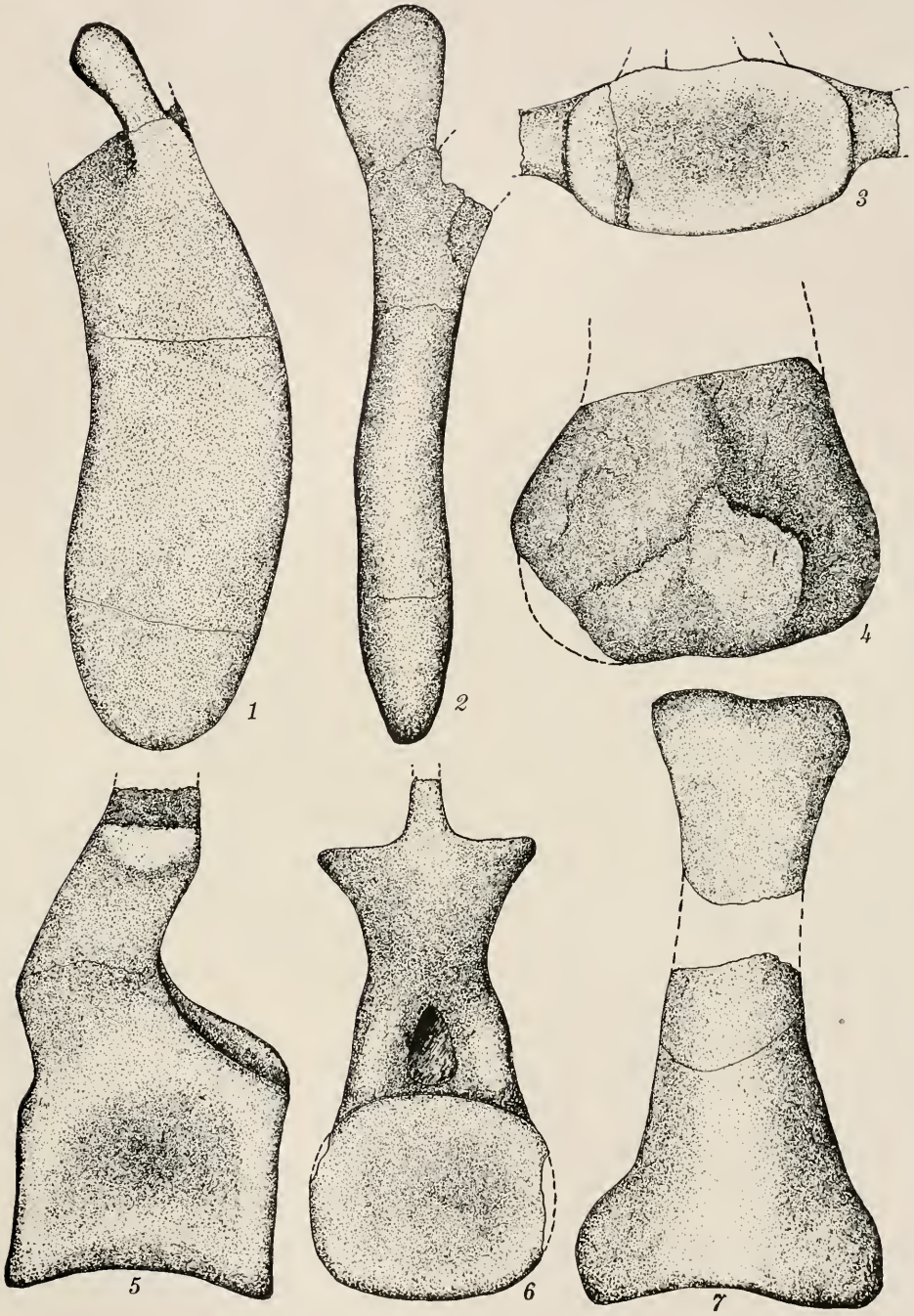
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PLATE LIX.

FIG. 1. Dorsal view of an anterior caudal vertebra. × ¼.

FIG. 2. A cross section of the sacrum to show the sacral enlargement. × ½.

FIG. 3. A small dermal spine. × ½.

FIGS. 4 and 5. Upper and lower portions of right fibula. × ¼.

FIGS. 6 and 7. Dorsal surface of posterior and anterior segments of the sacrum.

FIG. 8. The left ulna seen from behind. One-tenth natural size.

FIG. 9. The left ulna seen from the side. One-tenth natural size.

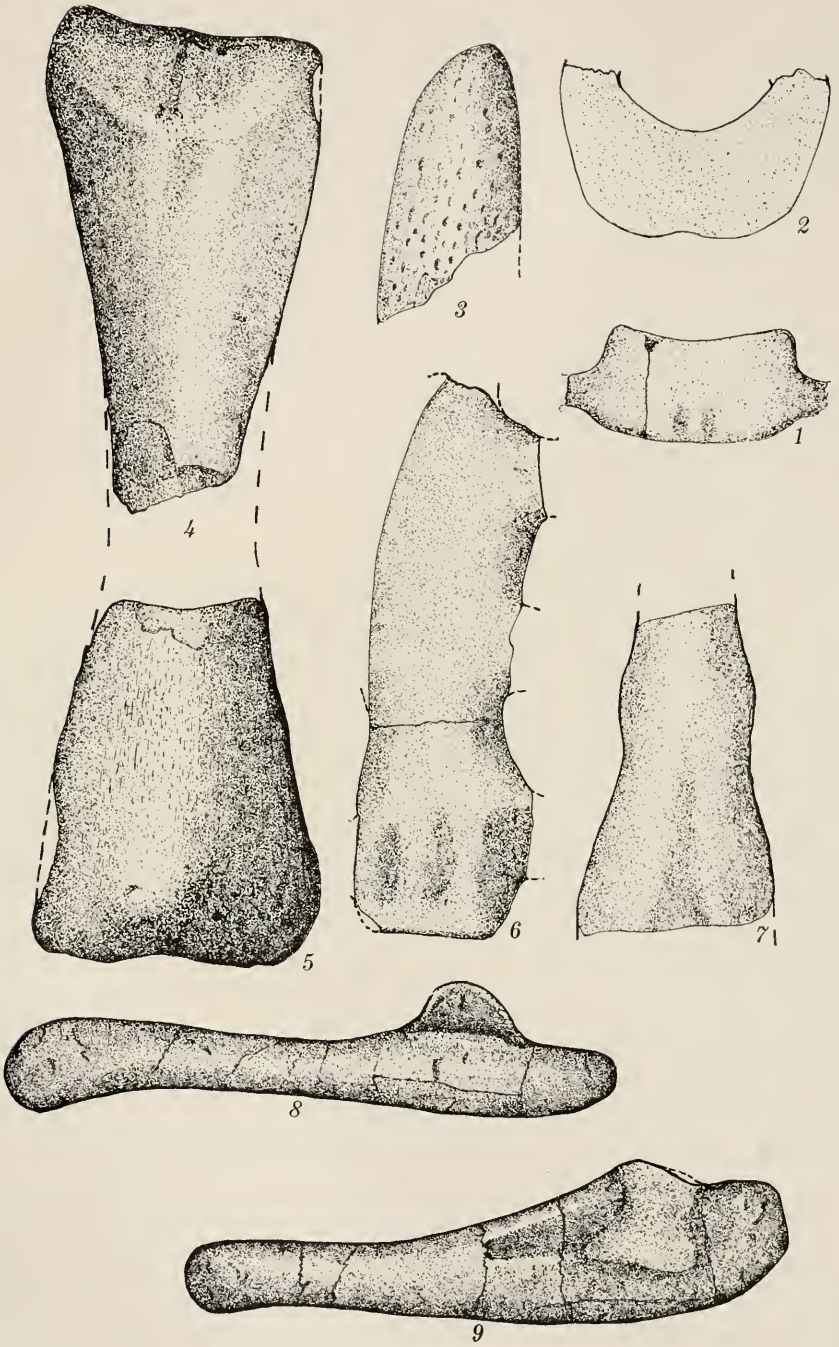
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Plate LX.

The stomach of *Empo nepaholica* Cope from the Niobrara Cretaceous. The longitudinal muscular plicæ are indicated by heavy lines. ×½.

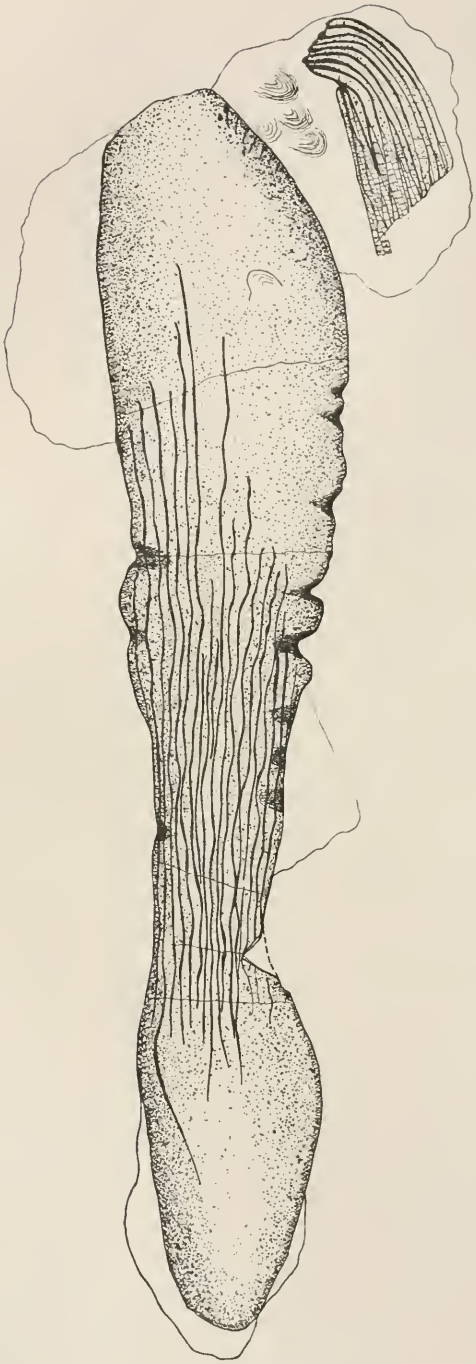


Plate LXI.

The specimen of *Thrissopater intestinalis* Moodie. × ⅔.

B 001

Plate LXII.

Fig. 1. Photograph of the alimentary canal of the Buffalo fish, *Ictiobus bubalus* Raf., from the Kaw river, showing the similarity in the form of the intestines to that preserved in the fossil *Thrissopater intestinalis* Moodie. $\times \frac{1}{2}$.

Fig. 2. Photograph of the right pectoral fin of *Empo nepaholica* Cope. $\times \frac{3}{4}$.

1

2

PLATE LXIII.

Upper figure: Lateral view of female of *Prorocorypha snowi*, new gen. and sp. × 2.

Second figure: Lateral view of male of *Prorocorypha snowi*. × 2.

Left of three middle figures: Lateral view of apex of male abdomen of *Prorocorypha snowi*. × 4. (The supra-anal plate of the specimen from which the artist made the drawing is broken. It is long, as in the female.)

Middle of three middle figures: Dorsal view of head and pronotum of female of *Prorocorypha snowi*. × 2.

Right of three middle figures: Lateral view of apex of female abdomen of *Prorocorypha snowi*. × 4.

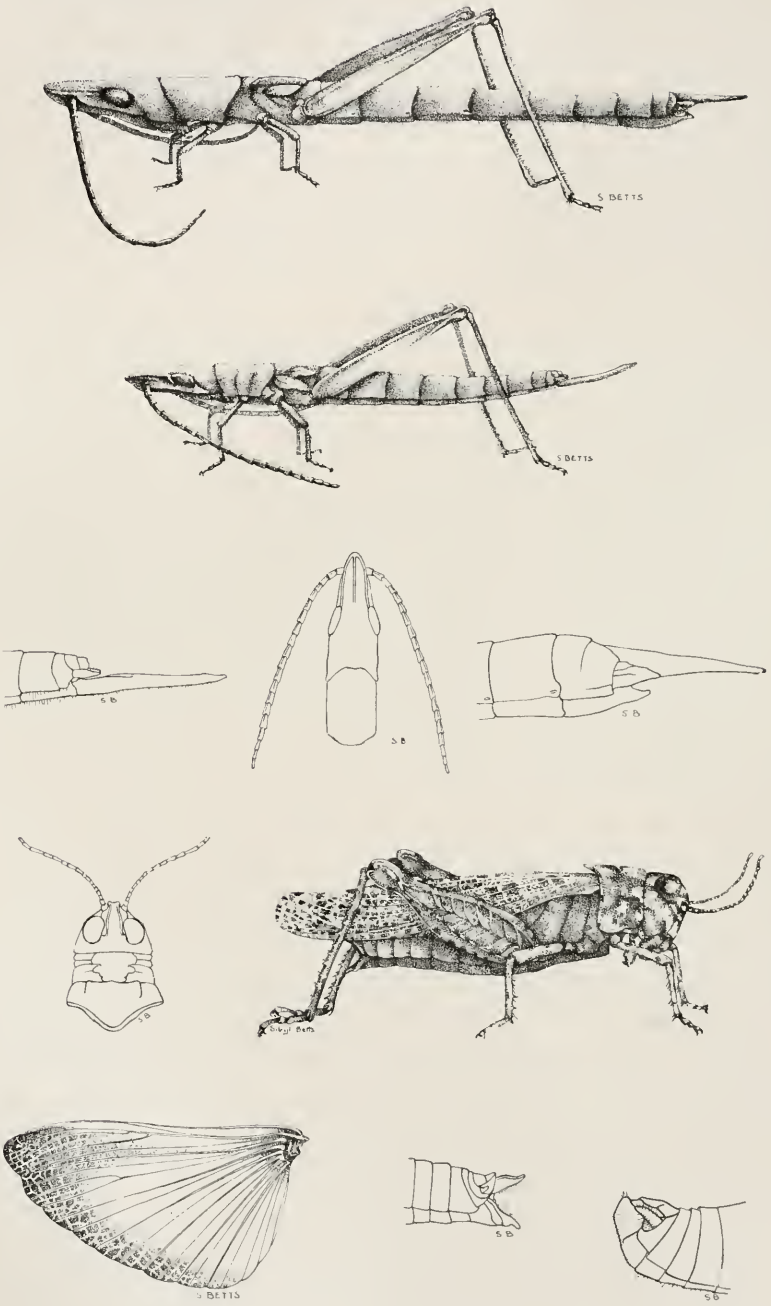
Next to bottom row, left figure: Dorsal view of head and pronotum of *Scirtetica ritensis*, new species. × 2.

Next to bottom row, right figure: Lateral view of type specimen of *Scirtetica ritensis*. × 2.

Bottom row, left figure: Wing of *Scirtetica ritensis*. × 2.

Bottom row, middle figure: Lateral view of apex of female abdomen of *Scirtetica ritensis*. × 2.

Bottom row, right figure: Lateral view of male abdomen of *Scirtetica ritensis*. × 2. (This figure was drawn by the artist from a specimen not studied by the author.)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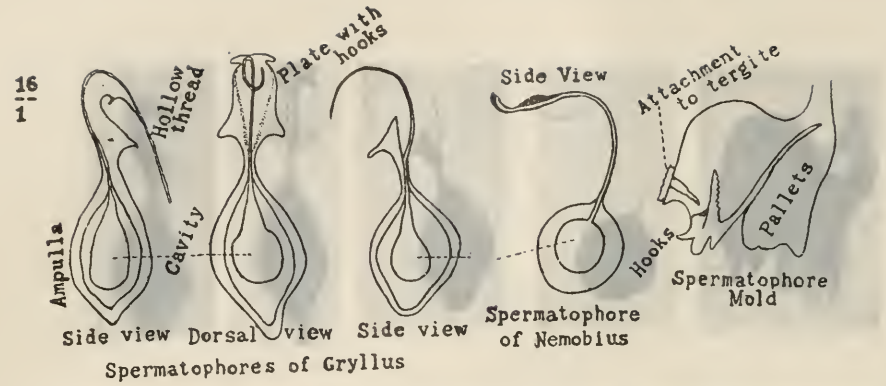
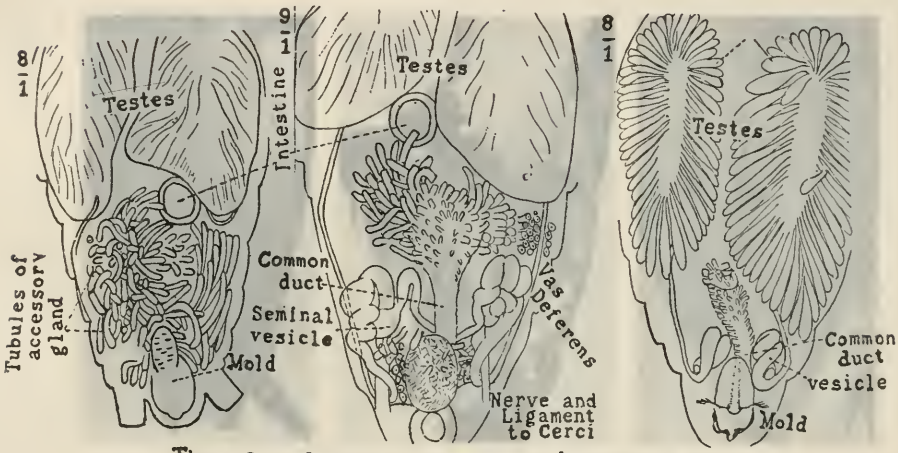
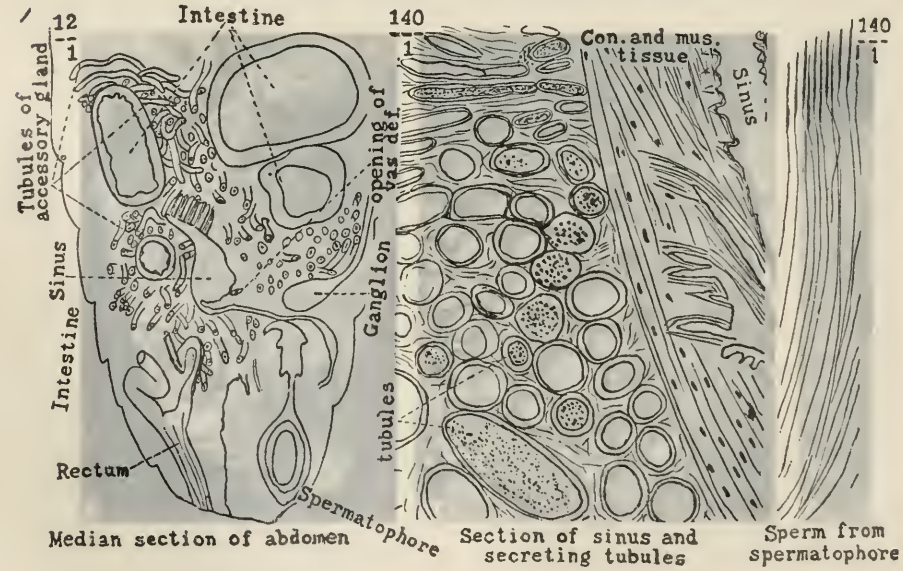


Spermatophores of Gryllus



Three Dorsal Dissections of the Abdomen of Gryllus



Median section of abdomen

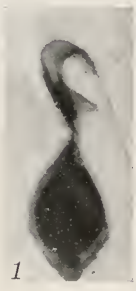
Section of sinus and secreting tubules

Sperm from spermatophore

Spermatophores of Gryllus
Side view
Dorsal view
Side view
Hollow head
Cavity
Hooks
Plate with hooks
Attachment to testis
Palpus
Hooks
Spermatophore Mold
Spermatophore of Nemobius
Side View

Three Dorsal Dissections of the Abdomen of Gryllus
Testes
Testes
Testes
Intestine
Common duct
Seminal vesicle
Mold
Vas deferens
Nerve and ligament to Cerci
Common Duct
vesicle
Mold
Ejac. duct
Accessory glands
To palpus

Intestine
To palpus
Accessory glands
Intestinal sinus
Rectum
Spermatophore
Median section of abdomen
Con. and mus. tissue
Sinus
Section of sinus and secreting tubules
Sperm from spermatophore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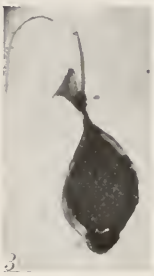
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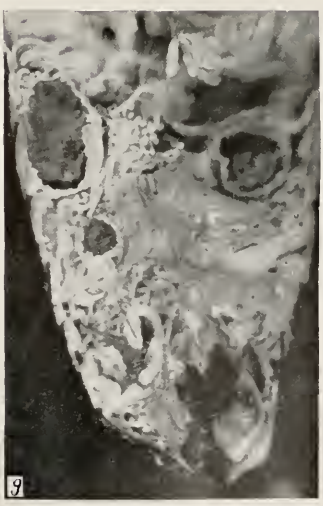
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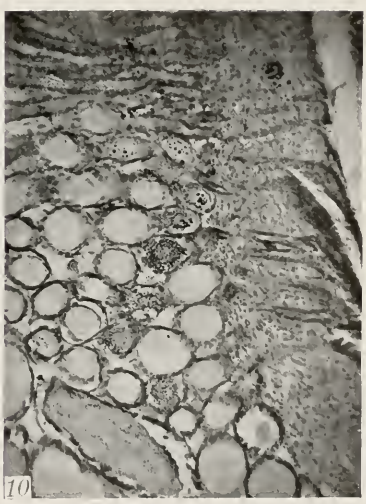
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PLATE LXV.

FIGS. 1 to 10, inclusive.—Polar views of the equatorial plate from spermatogonial cells, each showing the entire number of chromosomes. In figs. 1, 2 and 4 the possible pairing of equal elements is shown. There are ten pairs. Nos. 1-1 are the largest two spermatogonial chromosomes, which form the largest chromosome of the spermatocyte group. No. 11 is unpaired, and is the accessory chromosome. In figs. 5 to 10, inclusive, the connecting bands of linin are not shown.

FIG. 11.—Lateral view of the spindle in metaphase from a young spermatogonial cyst.

FIG. 12.—Same from an older spermatogonial cyst.

FIG. 13.—Beginning anaphase from an older spermatogonial cyst, showing the usual confluent condition of the chromatin.

FIG. 14.—Late spermatogonial anaphase.

FIG. 15.—A section of an entire spermatogonial cyst, showing the cells in different stages of division. The polarity shown is typical.

FIG. 16.—Early spermatogonial telophase.

FIG. 17.—Polar view of the same, in which all twenty-one members of the complex can be distinguished. (x) Accessory chromosome.

FIG. 18.—Late telophase, from a young spermatogonial cyst.

FIGS. 19 and 20.—Nuclei of spermatogonial cells, showing the chromatin at the point of greatest diffusion. The reticular structure is still evident.

FIG. 21.—A typical spermatogonial nucleus, showing the beginnings of the reorganization of the nuclear chromatin.

FIGS. 22 to 28, inclusive.—Successive stages in the re-formation of the spermatogonial chromosomes.

FIGS. 29 to 33, inclusive.—Nuclei in the process of synizesis. (x) Accessory chromosome. (t) Nuclear membrane. (c) Chromatin mass.

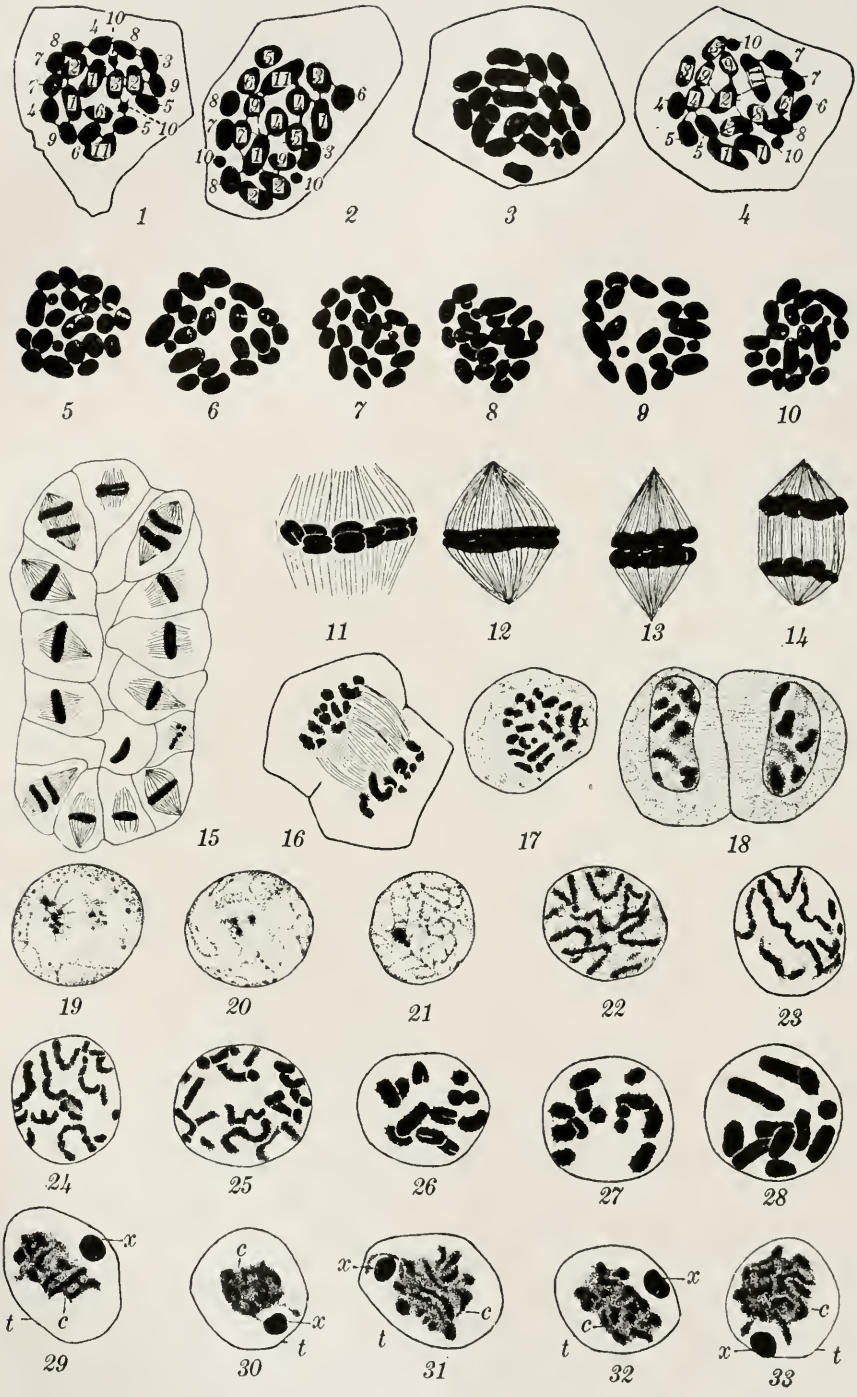
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PLATE LXVI.

FIG. 1.—An early stage of the spermatocyte nucleus, succeeding synizesis. (*x*) Accessory chromosome. (*p*) Plasmasome.

FIGS. 2 and 3.—Same as fig. 1.

FIG. 4.—Slightly later stage of the spermatocyte nucleus than is shown in figs. 1, 2 and 3. The chromatin is more diffuse and the accessory chromosome (*x*) is elongated, granular, and stains more deeply than the other chromatin.

FIG. 5.—A spermatocyte nucleus at the period of greatest diffusion. The chromatin is reticular. (*p*) Plasmasome. (*x*) Accessory chromosome more condensed than the form shown in fig. 4.

FIG. 6.—Same as fig. 5. The accessory is a homogeneous chromatin rod and the plasmasome reaches its maximum size in this stage.

FIG. 7.—Spermatocyte nucleus in early prophase, showing the first signs of chromosome reorganization. (*p*) Vacuolated plasmasome. (*x*) Accessory chromosome. The difference in the consistency of these two bodies is apparent in iron-hæmatoxylin preparations which were stained for a shorter time, comparatively, or which were subjected to a longer extraction process.

FIG. 8.—Spermatocyte nucleus, showing the beginnings of tetrad formation and the accompanying phenomenon, the decrease in size of the plasmasome.

FIG. 9.—Later spermatocyte prophase. The plasmasome becomes spherical as it disappears.

FIGS. 10 and 11.—Two parts of the same nucleus drawn from adjacent sections. There are thirteen bodies, all of which are shown. The plasmasome has diminished greatly in size. (*m*) The univalent halves of the small chromosome.

FIGS. 12 and 13.—Spermatocyte cells in early prophase. The nuclear wall in fig. 12 is not shown. The plasmasome is very lightly stained, in marked contrast to the accessory, which holds the stain much longer.

FIG. 14.—Accessory chromosomes drawn from spermatogonial cells in metaphase. For the method of identification see text.

FIG. 15.—Accessory chromosomes from cells of the same stage and preparation as that of fig. 12, where there is no trouble in identifying this element.

FIG. 16.—Tetrads from the same stage and preparations as figs. 12 and 13. (*a*) Largest form. (*b*) and (*c*) Typical forms of the cross. (*d*) The small chromosome, the halves of which are not usually so close together at this time.

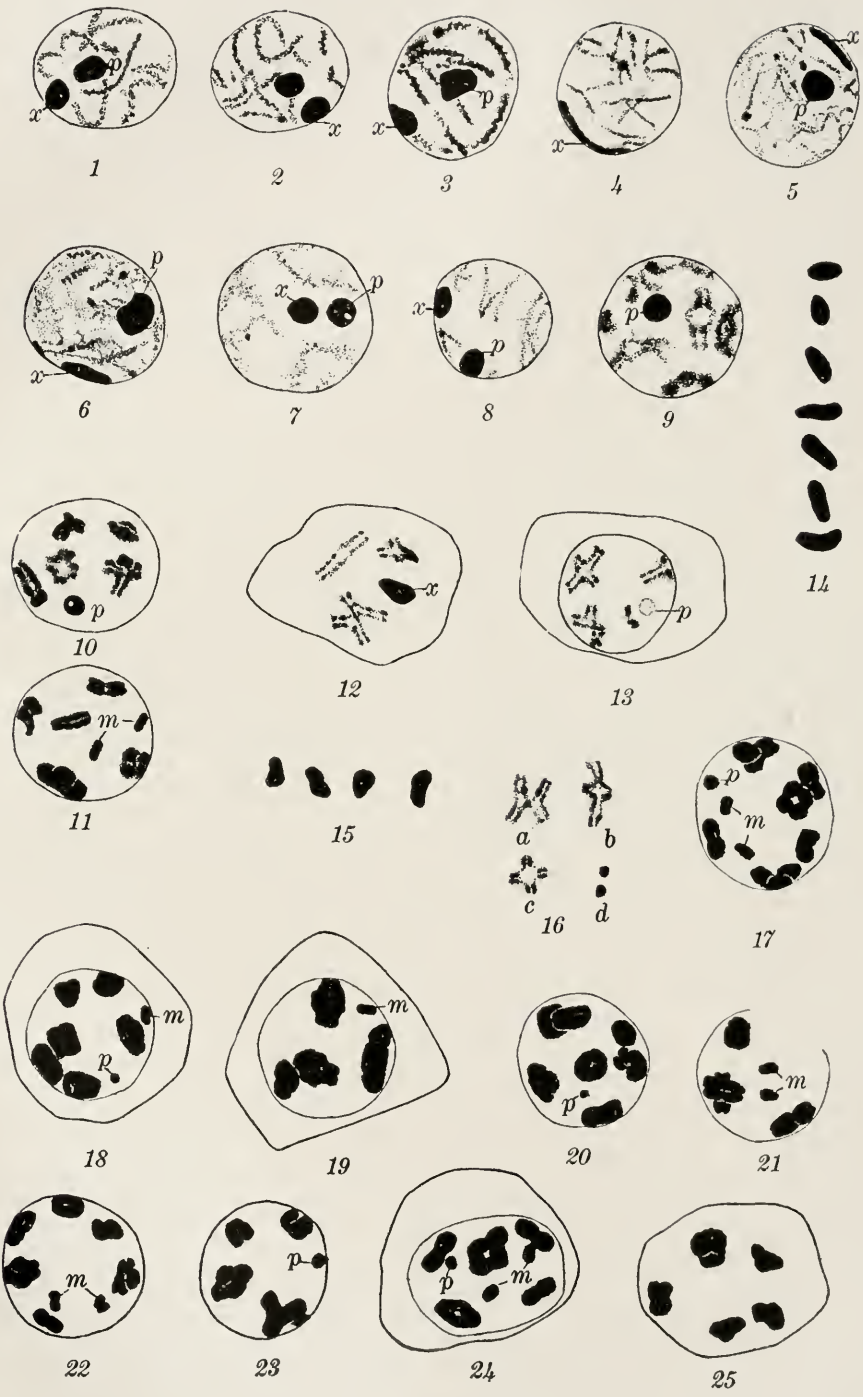
FIG. 17.—Portion of a spermatocyte nucleus in late prophase, showing the diminishing plasmasome (*p*) and the halves of the small chromosome (*m*).

FIGS. 18 and 19.—Portions of the same spermatocyte nucleus appearing in adjacent sections, showing thirteen elements—nine tetrads, two *m*-chromosome diads, the accessory chromosome, and the plasmasome. The plasmasome has almost entirely disappeared.

FIGS. 20 and 21.—Same as figs. 18 and 19.

FIGS. 22 and 23.—Same as the two previous figures.

FIGS. 24 and 25.—Same as above. The nuclear wall in fig. 25 is not shown.


p
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14
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m
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a
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c
d
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PLATE LXVII.

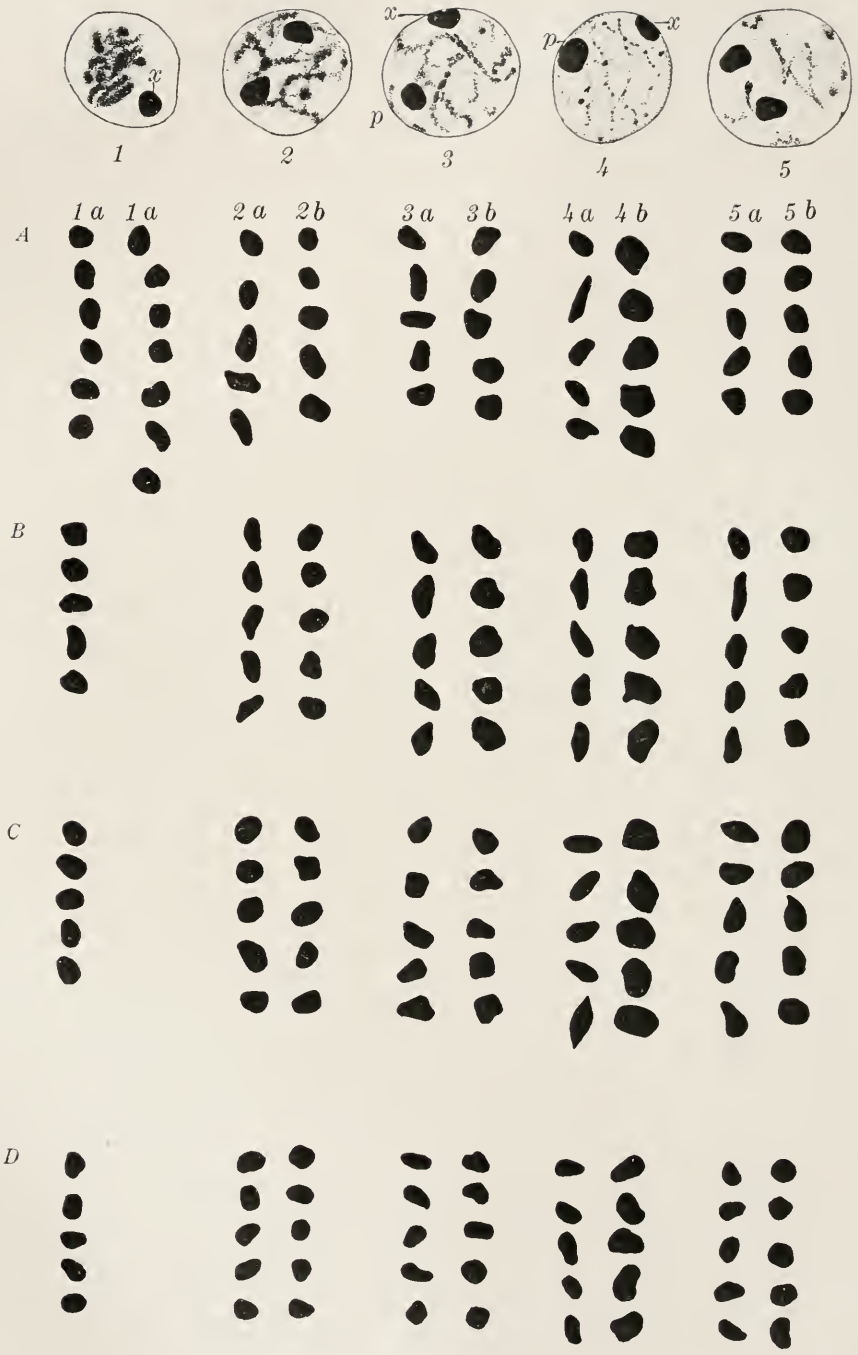
FIG. 1.—Nucleus in the process of synizesis. (x) Accessory chromosome. 1*a*.—Drawings of accessory chromosomes from nuclei similar to fig 1. *A*, *B*, *C* and *D* indicate the four individuals from which these comparative drawings were made.

FIG. 2.—Spermatocyte nucleus, immediately after synizesis, showing both accessory chromosomes and the plasmasome. 2*a*.—Accessory chromosomes from the same stage as is shown in fig. 2. 2*b*.—Plasmasomes from the same nuclei as the accessory chromosomes in 2*a*. The opposite elements in columns 2*a* and 2*b* are from the same nucleus. The same holds true for columns 3*a* and 3*b*, 4*a* and 4*b*, 5*a* and 5*b*.

FIG. 3.—Spermatocyte nucleus, showing a later stage than fig. 2. 3*a*.—Accessory chromosomes from the same stage as fig. 3. 3*b*.—Plasmasomes from the same stage as fig. 3. See explanation of fig. 2, same plate.

FIG. 4.—Spermatocyte nucleus at the period of maximum diffusion and largest plasmasome growth, deeply stained. 4*a*.—Accessory chromosomes from same state as fig. 4. 4*b*.—Plasmasomes from same stage as fig. 4. See explanation of fig. 2, same plate.

FIG. 5.—Spermatocyte nucleus, showing the beginning of chromosome reorganization. 5*a*.—Accessory chromosomes from the same stage as fig. 5. 5*b*.—Plasmasomes from the same stage as fig. 5. See explanation of fig. 2, same plate.


x
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2a 2b
3a 3b
4a 4b
5a 5b
A
B
C
D

PLATE LXVIII.

FIGS. 1 to 10, inclusive.—The chromosome complex of the first spermatocyte in metaphase. (x) Accessory chromosome.

FIG. 5.—An unusual condition of the first spermatocyte metaphase, showing twelve elements. a-a.—Probably the disjoined halves of one of the larger chromosomes which normally occurs in the ring.

FIG. 11.—Drawings of the accessory chromosome from cells of the cyst from which fig. 6 was made, showing the constancy in size in this element within a single cyst.

FIG. 12.—Drawings of the accessory chromosome from cells of the cyst from which fig. 7 was made.

FIG. 13.—Drawings of the accessory chromosome from cells of the cyst from which fig. 8 was made.

FIG. 14.—Drawings of the accessory chromosome from cells of the cyst from which fig. 9 was made.

FIG. 15.—Drawings of the accessory chromosome from cells of the cyst from which fig. 10 was made.

FIG. 16.—Lateral view of first spermatocyte in beginning anaphase. (x) Accessory chromosome. The cell membrane is shown.

FIG. 17.—First spermatocyte spindle, in longitudinal section through the accessory chromosome (x). (a) and (b) Chromosomes of the ring at equal distances from (m), the central small chromosome. The accessory chromosome lies outside of the ring, causing the asymmetry of the spindle, as drawn.

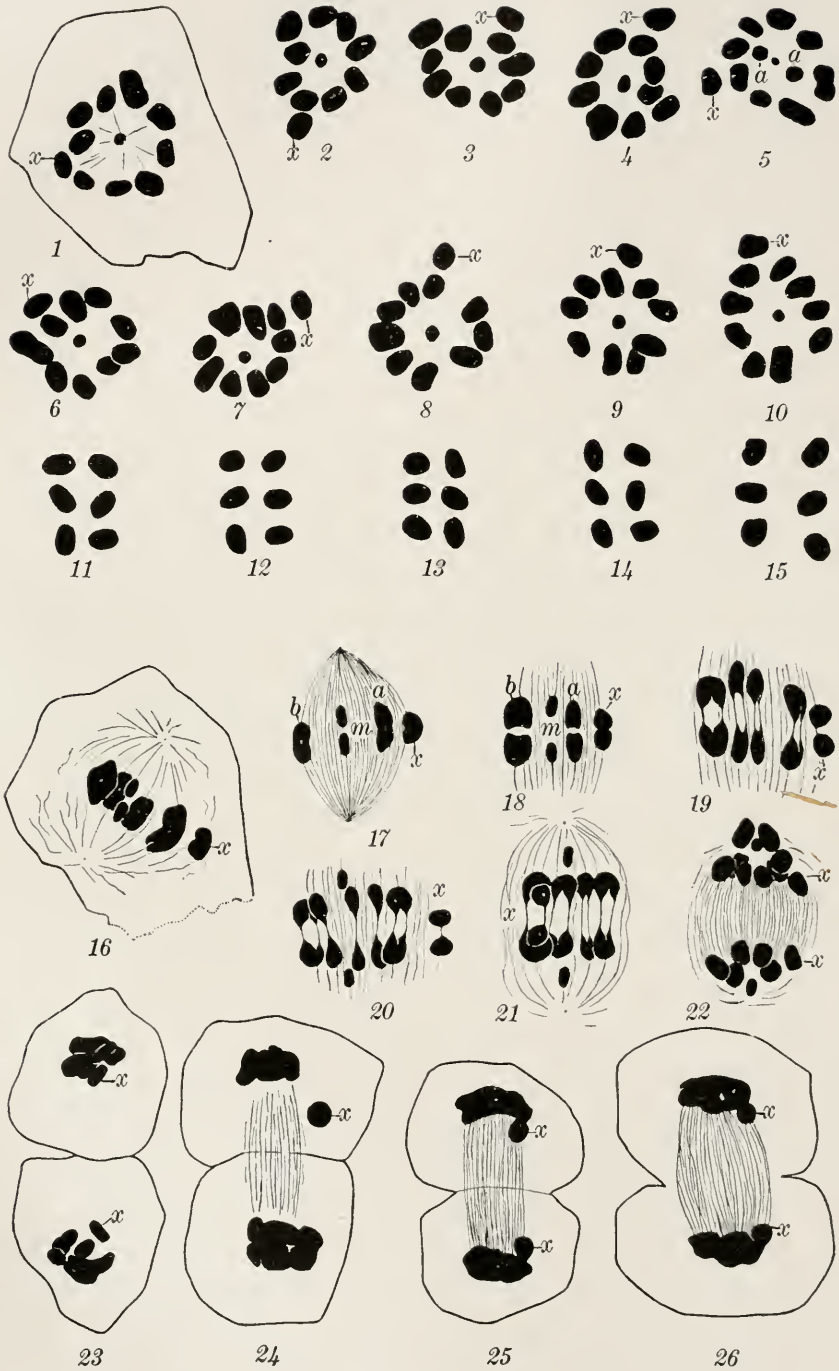
FIG. 18.—Same view of a slightly later stage, showing the typical irregularity in the movements of the accessory chromosome (x) and the central small chromosome (m) with respect to those of the ring (a) and (b).

FIG. 19.—Later anaphase, showing the difference in organization between the accessory chromosome (x) and the ordinary chromosomes.

FIGS. 20, 21 and 22.—Later successive stages of the first spermatocyte anaphase. (x) Accessory chromosome.

FIGS. 23, 25 and 26.—First spermatocyte telophases, in which the accessory chromosome (x) may still plainly be identified.

FIG. 24.—Telophase of first spermatocyte. (x) Unusual element, which is probably an undivided accessory chromosome or a persistent plasmasome.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x
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PLATE LXIX.

FIGS. 1, 2 and 3.—Polar views of the single daughter groups of chromosomes resulting from the first spermatocyte division. This stage is of very brief duration following immediately that in figure 25, plate LXVIII.

FIG. 4.—A group of drawings of the accessory chromosome from stages such as are shown in figures 1, 2 and 3.

FIGS. 5, 6, 7 and 8.—Polar views of the second spermatocyte complex. Note difference in arrangement of the chromosomes compared with those of first spermatocytes.

FIG. 9.—Oblique view of a late first spermatocyte telophase. One whole daughter group is shown and part of the other.

FIGS. 10, 11 and 12.—Lateral view of second spermatocyte spindle in metaphase. (x) Accessory chromosome. (m) Small central chromosome.

FIG. 13.—Lateral view of early anaphase, second spermatocyte.

FIG. 14.—Later stage of the same. (x) Accessory chromosome.

FIG. 15.—Same as figures 13 and 14, showing all of the chromosomes. (x) Accessory chromosome.

FIG. 16.—Same as figure 14.

FIG. 17.—Slightly later stage, showing the beginnings of the formation of a dividing cell membrane. Note that the daughter groups of chromosomes are entirely coalesced. This is typical of these later stages.

FIG. 18.—Same as figure 14.

FIG. 19.—Group of accessory chromosomes drawn from cells such as are shown in figure 18, showing the constancy in size of the lagging element (x).

FIGS. 20, 21, 22, 23, 24 and 25.—Later stages in the second spermatocyte division, showing the behavior of the accessory chromosome (x). Note the dividing cell wall and persistent spindle fibers which identify beyond a doubt the two cells shown in each figure as daughter cells of the same first spermatocyte.

FIGS. 26 and 28.—Later stage of the same after the formation of the nuclear membranes. (x) Accessory chromosome.

FIG. 27.—Later stage of the same in which the spindle fibers are fading.

FIG. 29.—Still later stage in which the two chromatin masses are breaking up and the ordinary chromatin appears granular. (x) Accessory chromosome.

FIG. 30.—A group of drawings, showing the typical appearance of the daughter nuclei of the second spermatocyte which have received the accessory chromosome in the second maturation division.

FIG. 31.—A group of drawings showing the early development of the spermatid which received the accessory chromosome in the second maturation division.

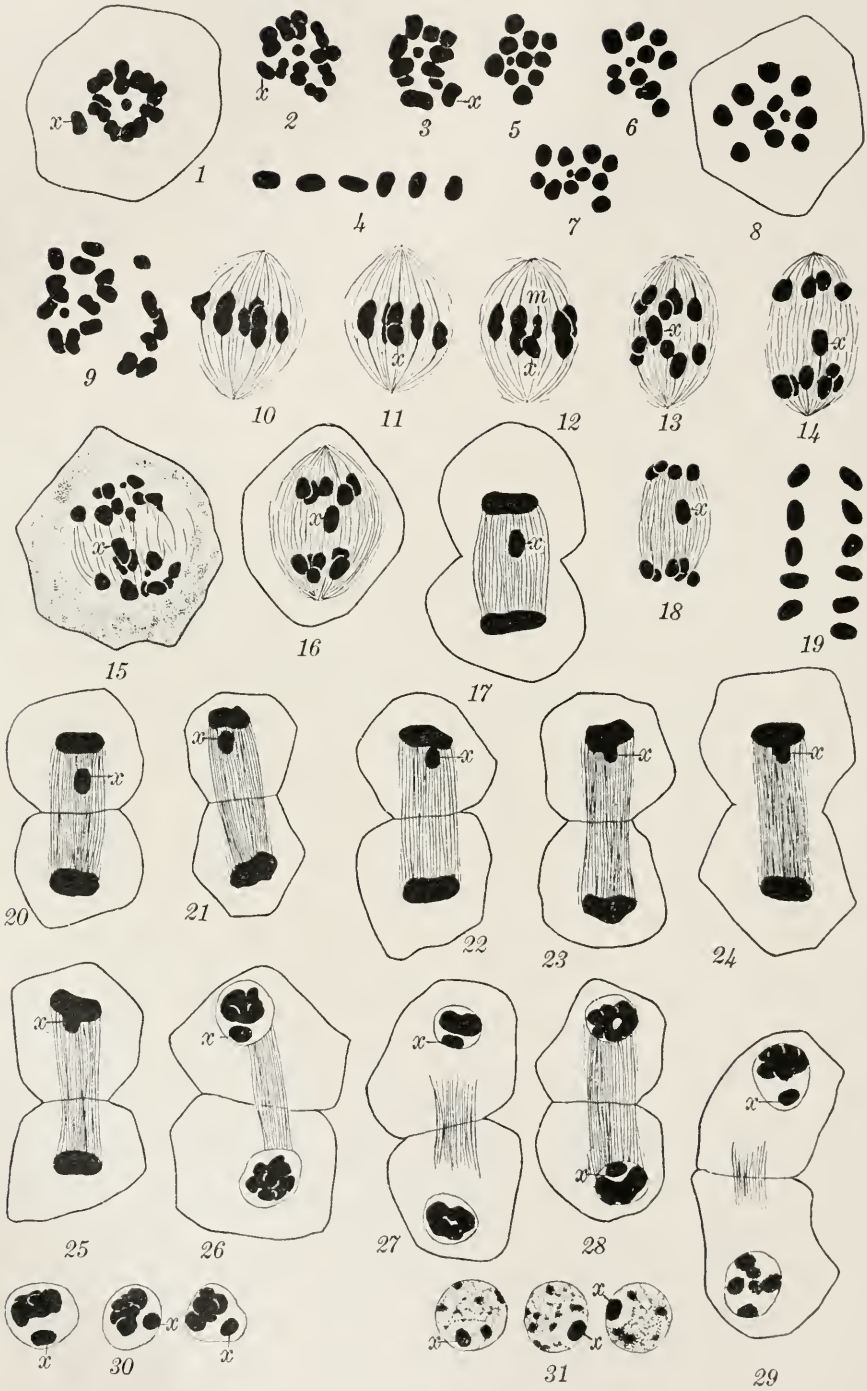
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PLATE LXX.

These photomicrographs were made with a Zeiss 2mm., 1.40 N. A. apochromatic objective and No. 4 projection ocular, the camera bellows being extended so as to place the sensitive plate at a distance of thirty-one inches above the object. Illumination was furnished by Welsbach mantle, the light passing through a Watson Parachromatic oil immersion condenser with the diaphragm set at N. A. 1.0. The original magnification is 1500 diameters which, in reproduction, has been reduced to 1000 diameters. Considerable detail has been lost in reproduction, especially in figures 3, 7 and 8.

FIG. 1.—Polar view of spermatogonial metaphase, showing 21 chromosomes.

FIG. 2.—Same as figure 1.

FIG. 3.—Same as figure 1.

FIG. 4.—First spermatocyte prophase, in which the accessory chromosome is bent in the middle. This is the nearest approach to the spireme condition found in *Anasa*.

FIG. 5.—Later prophase with the accessory extended and showing the longitudinal split.

FIG. 6.—Same stage as in figure 5.

FIG. 7.—A portion of three cysts appears in this photograph. In the lower one the last generations of spermatogonial chromosomes are seen in several cells. At the upper right-hand corner are four cells in synizesis.

FIG. 8.—Parts of three cysts are included in this picture. The cells in each are in some stage of synizesis. The presence of the accessory chromosome on the periphery of the nucleus and of the plasmasome in the synizetic knot is demonstrated in several cells. The stages shown in figures 7 and 8 precede the ones represented in figures 4, 5 and 6.

FIG. 9.—Post-synizetic stage, in which the peripheral accessory and the more central plasmasome are shown in several cells. This may be compared with a similar condition in cells prepared according to the method of Foot and Strobell, as shown in their figures 11 and 12, in order to judge of the correctness of their belief that the smear method preserves delicate detail better than sections. It may be pointed out also that there is little liability to confuse either of the nucleolar bodies with karyosomes resulting from concentrations of the chromatin elsewhere. Wilson's slide 949*b*. Photos 1 to 9 from sections.

FIG. 10.—Chromosomes of the first spermatocyte metaphase, smear preparation. The lowermost chromosome is the accessory. It is seen to have one plane of division, while the others have more or less distinct second planes indicated. In this cell the five lower chromosomes have dried thinner and spread more than the upper six and show wrinkles and other distortions. Wilson's Woods Hole "x" slide.

FIGS. 11-15.—Photographs from sections on Wilson's slide 949*b*, showing the accessory chromosome and plasmasome in the first spermatocyte prophase at about the same stage as that of figure 9. It is difficult to

get several nuclei close together with the two elements in focus at the same time, but most of these show at least two cells. Figure 11 is in focus at the level of the upper part of the nucleus and shows the accessory extended as in figures 5 and 6.

FIGS. 16-20.—Photographs from smears on Lefevre's slide 30, showing the late prohases of the first spermatocyte. The accessory is distinguished, as Foot and Strobell point out, by having two halves lying side by side without lateral extensions. There is no indication of a second plane of division, as may easily be seen in figures 16 and 20. In figure 20 there appear thirteen elements.

FIGS. 21-26. These are from smears, and show the chromosomes of the first spermatocyte in metaphase. The great difference in the size of the chromosomes, due to the variation in the extent of spreading, upon drying may be judged by comparing figure 22 with figures 23 and 10. In figure 23 there are twelve elements, one much lighter than the others, which may be interpreted as an unsually resistant plasmasome which has persisted much longer than common. In all of these the accessory may be identified both by its position and by the single plane of cleavage indicated. It has been injured in the cell represented in figure 23, where it is seen next to the plasmasome with one corner cut sharply off.

FIGS. 27 and 28.—Photographs of the first spermatocyte metaphase, polar view, showing the typical arrangement of the chromosomes. The accessory lies without the ring and the *m*-chromosome in the center. These prints are from the *same negative* and show how it is possible to vary the apparent size of structures even by printing. Wilson's section.

FIGS. 29-33.—Polar views of first spermatocyte metaphases from sections. In order to get several cells to show together the focus was shifted during exposure in making photograph 31 so that the outlines are not sharp. In figure 29 the accessory does not show, being just out of focus in the lower cell. From these illustrations it may be seen that while there is a general agreement in the arrangement of the chromosomes in the equatorial plate, it may be modified in details. Wilson's sections.

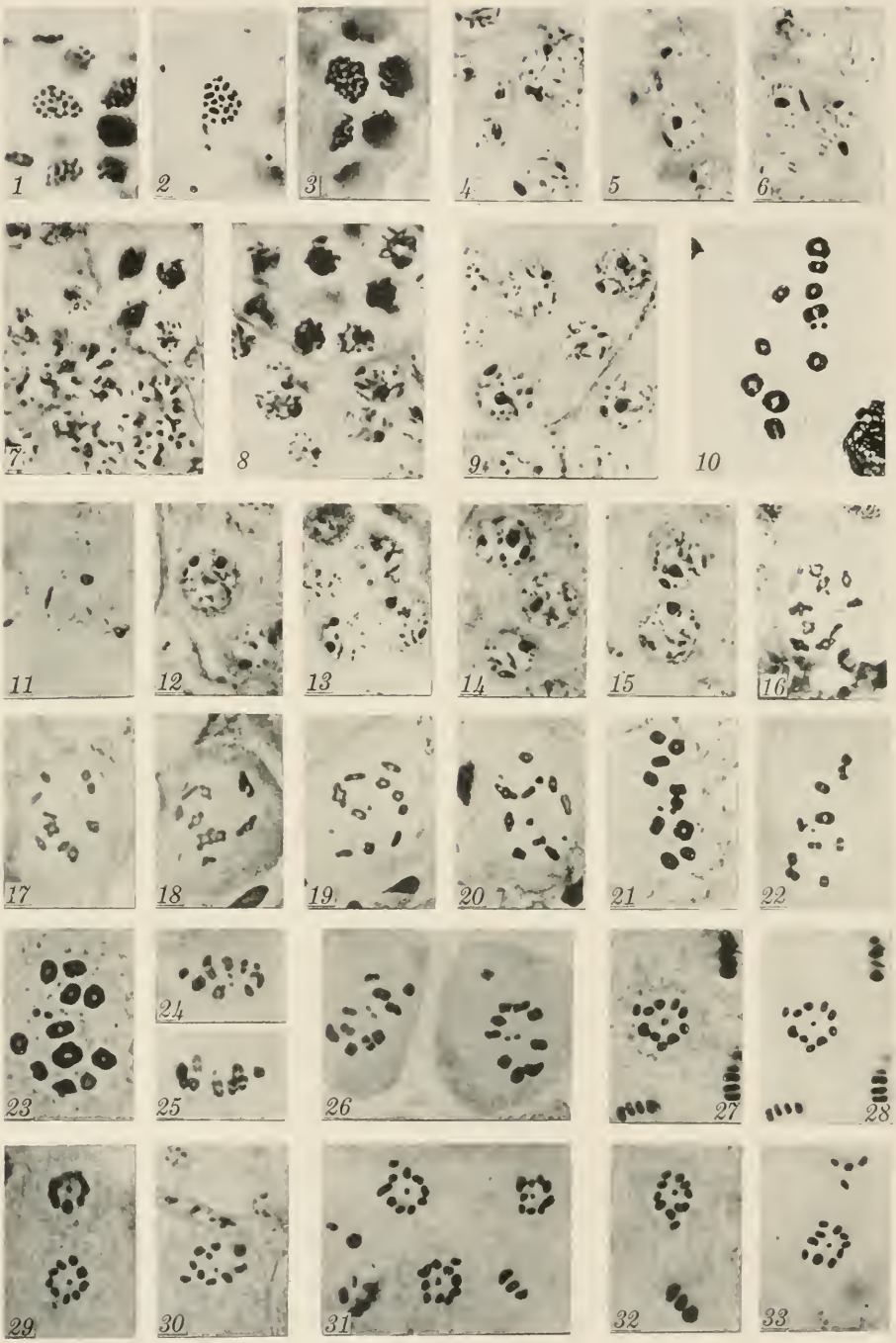

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PLATE LXXI.

FIG. 1.—Lateral view of two second spermatocytes in early anaphase. It is apparent in both of these that the accessory chromosome is already in movement to one of the poles, in the upper cell to the right and in the lower to the left. The accessory in the upper cell already has its longer axis parallel to that of the spindle. Smear by Wilson.

FIG. 2.—Lateral view of first spermatocyte in metaphase or early anaphase. The accessory is the lowermost chromosome. All the elements are clearly seen to be divided. This is a slightly earlier stage than the ones of the second spermatocytes in figure 1 and should be compared with them in order to see the difference in the behavior of the accessory in the two divisions. Smear by Lefevre.

FIG. 3.—Mid-anaphase of the first spermatocyte, showing the full complex of chromosomes in each daughter cell. The accessory is the lowermost one in each group and is slightly removed from the others. Smear by Wilson.

FIG. 4.—Late anaphase of the first spermatocyte mitosis. The accessory lies to the right of each daughter group at the same level. Smear by Lefevre.

FIG. 5.—Mid-anaphase of the first spermatocyte, oblique view. The accessory to the right of each daughter group.

FIG. 6.—Mid-anaphase of the first spermatocyte anaphase, lateral view. The accessory at the lower end of each daughter group.

FIG. 7.—Very late anaphase of the first spermatocyte division, lateral view, with the accessory chromosome of each group proximal to the equatorial plate. Smear by Wilson.

FIG. 8.—Late anaphase of the first spermatocyte mitosis, showing the divided accessory accompanying each daughter group of chromosomes. Smear by Lefevre.

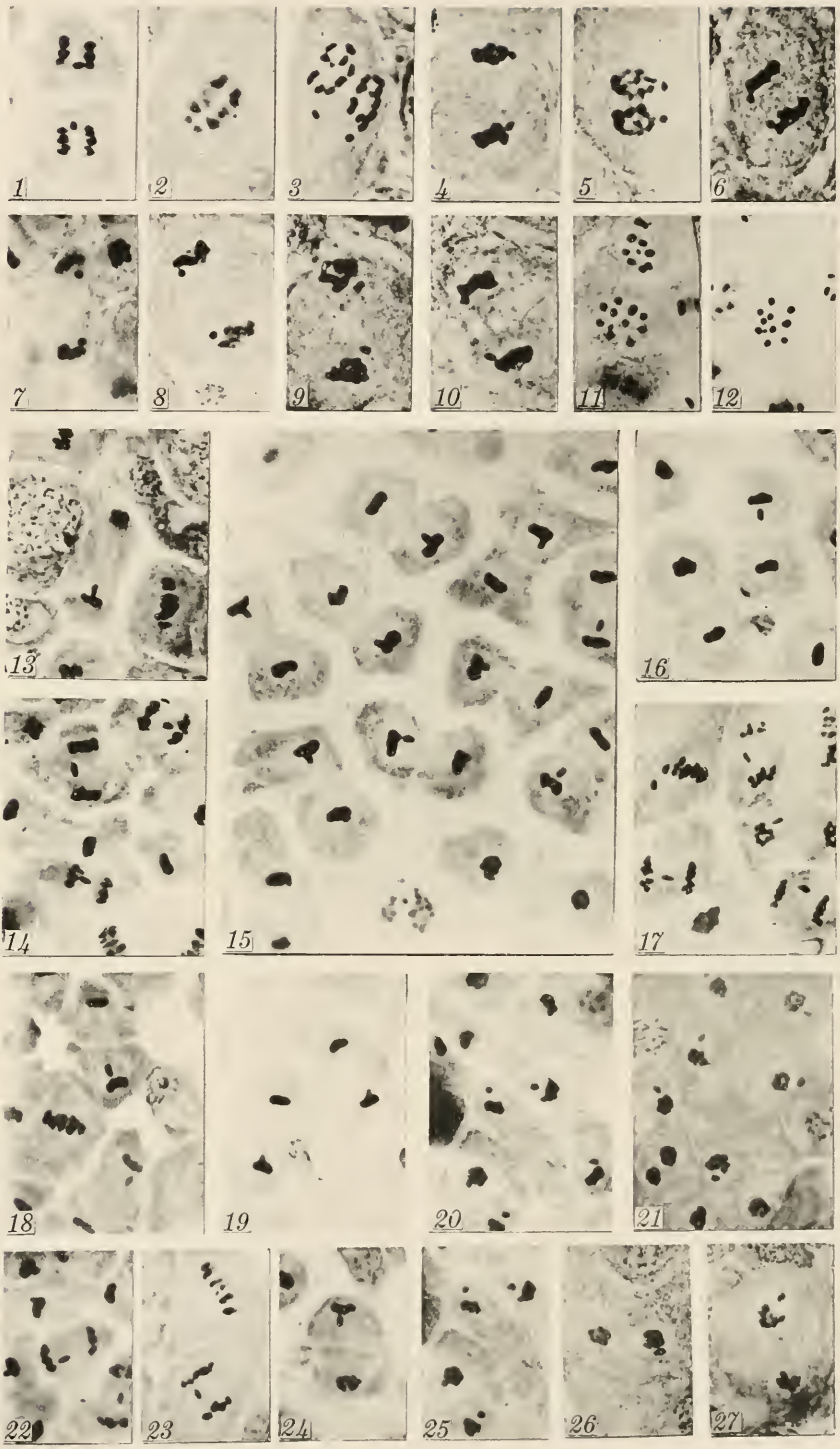
FIG. 9.—Like figure 8. Smear by Lefevre.

FIG. 10. Similar to figures 8 and 9. Smear by Lefevre. This series of anaphases of the first spermatocyte indicate, I think, that the accessory is characterized by an independence of movement and position in the group of chromosomes rather than by a "lagging" tendency. It does not in any case, apparently, anticipate the poleward movement of the other chromosomes, but takes part in the general division. On account of its peripheral position and slighter relation to the plate of chromosomes it is crowded back and therefore lies below the daughter mass of chromatin. Its position in the metaphase of the second spermatocyte depends upon the degree to which it is crowded aside in the telophase of the first. If it maintains its peripheral position at the level of the other chromosomes it is then an eccentric element in the metaphase of the second spermatocyte. If, however, it lies beneath the other chromosomes in the telophase it may become included within the ring of chromosomes in the next metaphase.

FIG. 11.—Polar view of second spermatocyte metaphase. In the lower cell three chromosomes are shown in lateral view. The difference in the arrangement of the chromosomes, as compared with the first spermatocyte, is striking and apparent. Section by Wilson.

FIG. 12.—Similar to figure 11. Compared with the cell shown in the preceding figure it is seen that the arrangement of the chromosomes is different and that both are unlike that of the first spermatocyte where the *m*-chromosome practically always lies within a ring of larger chromosomes. The upper cell in figure 11 shows how close the resemblance to the first spermatocyte may be, on the contrary. Section by Wilson.

FIGS. 13-27.—Photomicrographs of smears, mostly from slides by Wilson, showing the behavior of the accessory in the second spermatocyte. It will appear from these, I think, that while the accessory may lie near the equatorial plate in the early and mid anaphases, when actual division of the cell has occurred the position of the accessory in only one of the two daughter cells may be determined. Of particular importance in this connection is figure 15 where numerous cells in telophase are in focus at one time. Each one of these demonstrates beyond question the unilateral movement of the accessory. This area is but a small part of a much larger one on the slide, where more than a hundred similar cells show, without exception, the same undivided condition of the unpaired element. The lagging chromosome is recognized by all to be the accessory. It is seen here in all the divided cells to pass without division into but one of the two daughter derivatives. In comparing these figures with those of Foot and Strobell it should be borne in mind that these cells are without question completely divided, that numbers of them are shown together, and that the whole cell body is represented, so that there can be no question of the relation between the members of the pairs of chromosome groups. Their figures, on the contrary, are of single cells, mostly in early or mid anaphases, in which the cell body does not appear. The consistent behavior of the accessory chromosome in the different cell generations is worthy of attention also. Wherever it is found it tends to isolate itself somewhat from the rest of the chromosomes and to behave with some independence. The argument of Foot and Strobell is based on conformity to one type on the part of the accessory as well as on that of the ordinary chromosomes. The figures on plate LXXI will demonstrate, I believe, that the accessory does not conform to the processes of the other chromosomes. Its isolated position in *one* of the two daughter spermatids shown in figures 26 and 27 is just as apparent as it is in *each* of the two daughter spermatocytes shown in figures 3-10. This characteristic may also be seen in figures 20, 21 and 25. Certain cells in the stages represented in figures 14, 17, 22, 23 may suggest that the accessory chromosome might later divide, and it is upon such as these that Foot and Strobell base much of their argument, but later and more decisive stages demonstrate that it does not do so and this positive evidence has much more value than the presumptive. It is my belief from a careful study of the material and the photographs of Foot and Strobell that not one instance which they figure is an indubitable case of a divided accessory in the second spermatocyte. I do not believe that the indentations in outline, or the light places in the middle of the accessory, have any value as an indication of probable division, for such effects must inevitably occur to delicate structures like the chromosomes in smearing. I would submit that if such evidence is to be used, the chromosomes of the upper group in the anaphase of the second spermatocyte represented in figure 37, plate III of Foot and Strobell, are much more certainly divided than are any of the accessories for which they claim divisions in figures 26-46 of the same plate.



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